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DENSITY AND ELEVATIONAL DISTRIBUTION OF THE SAN FRANCISCO PEAKS RAGWORT, *PACKERA FRANCISCANA* (ASTERACEAE), A THREATENED SINGLE-MOUNTAIN ENDEMIC

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ABSTRACT

Packera franciscana (Greene) W. A. Weber and A. Löve is endemic to treeline and alpine habitats of the San Francisco Peaks, Arizona, USA and was listed as a threatened species under the Endangered Species Act in 1983. Species abundance data are limited in scope, yet are critical for recovery of the species, especially in light of predictions of its future extinction due to climate change. This study defined baseline population densities along two transects which will allow the detection of future population trends. *Packera franciscana* ranged from 3529 to 3722 m elevation along the outer slope transect and densities were 4.18 and 2.74 ramets m^{-2} in 2008 and 2009, respectively. The overall *P. franciscana* 2009 density estimate for both transects was 4.36 ramets m^{-2} within its elevational range of occurrence, 3471–3722 m. The inner basin density was higher, 5.62 ramets m^{-2} , than the estimate for outer slopes, 2.89 ramets m^{-2} . The elevation of the 2009 population centroid for both transects was at 3586 (± 10 SE) m with the inner basin centroid significantly lower than the outer slopes centroid: 3547 (± 7 SE) m vs. 3638 (± 7 SE) m, respectively. In mid-September, 6–9% of the *P. franciscana* ramets were flowering and/or fruiting in 2008–2009. These results and our estimate of $>36,000$ *P. franciscana* ramets in $<2\%$ of its range would suggest that the species is locally abundant, persisting and reproducing.

Key Words: Alpine, narrow endemic, *Senecio franciscanus*, talus, trail transect.

Packera franciscana (Greene) W.A. Weber and A. Löve (Asteraceae), San Francisco Peaks ragwort, is endemic to treeline and alpine habitats of the San Francisco Peaks in Arizona (Greenman 1917; Barkley 1968; Trock 2006) (Fig. 1) where it has been reported to mostly occur between 3525 and 3605 m elevation (Dexter 2007) or, more generally, 3200–3800 m (Trock 2006). *Packera franciscana* predominately inhabits loose talus slopes (USFWS 1983) and has a reported range size of 85 ha (Dexter 2007). Since the elevation of the highest peak on the mountain is 3854 m, there is little habitat available for the plant to migrate upward in a warming climate scenario, and it has been widely speculated that the species is vulnerable to extinction due to climate change. In 1985, the distribution of *P. franciscana* on the San Francisco Peaks was mapped (Dexter 2007), but little published data is available on species abundance. *Packera franciscana*, as *Senecio franciscanus* Greene (Greene 1889), was listed as a threatened species under the Endangered Species Act by the U.S. Fish and Wildlife Service (1983) due to its narrow geographic distribution, apparent habitat specificity, and concerns over recreational impacts. Four other *Packera* taxa primarily grow in alpine–subalpine talus habitats in western America and two of those, *Packera musiniensis* (S. L. Welsh) Trock and *Packera malmstenii* (S. F. Blake ex Tidestrom) Kartesz, are also of conservation concern (FNA 1993+). The evolutionary rela-

tionships of *P. franciscana* within *Packera* are unknown.

Global mean temperature is predicted to rise 1–6°C in the next century due to increased concentration of greenhouse gases (Solomon et al. 2007) and has increased 0.4°C over the previous 150 yr (Trenberth et al. 2007). The predicted general response of species to this increased warmth is to migrate north in latitude or up in altitude (Grabherr et al. 1994; Theurillat and Guisan 2001; Walther 2002; Root et al. 2003; Kullman 2008; Lenoir et al. 2008). Alpine species population decline and extinction are also possible since there may be little available habitat for species' upward migration (Chapin and Körner 1994; Grabherr et al. 1994; Theurillat and Guisan 2001). These potential ecological changes indicate the need to establish baseline plant species' distributions and abundances at local scales to definitively detect changes (Post et al. 2009). Locally abundant, single mountain endemic species offer good opportunities to establish baseline studies for this purpose.

Kruckeberg and Rabinowitz (1985) note that narrow endemics can be locally abundant in specific habitats but geographically restricted. Biologists have long observed that *P. franciscana* is common to abundant in the alpine of the San Francisco Peaks (Greene 1889; Little 1941; Phillips and Peterson 1980; USFWS 1983; Phillips and Phillips 1987; Trock 2006), but peer-reviewed studies of *P. franciscana* abun-

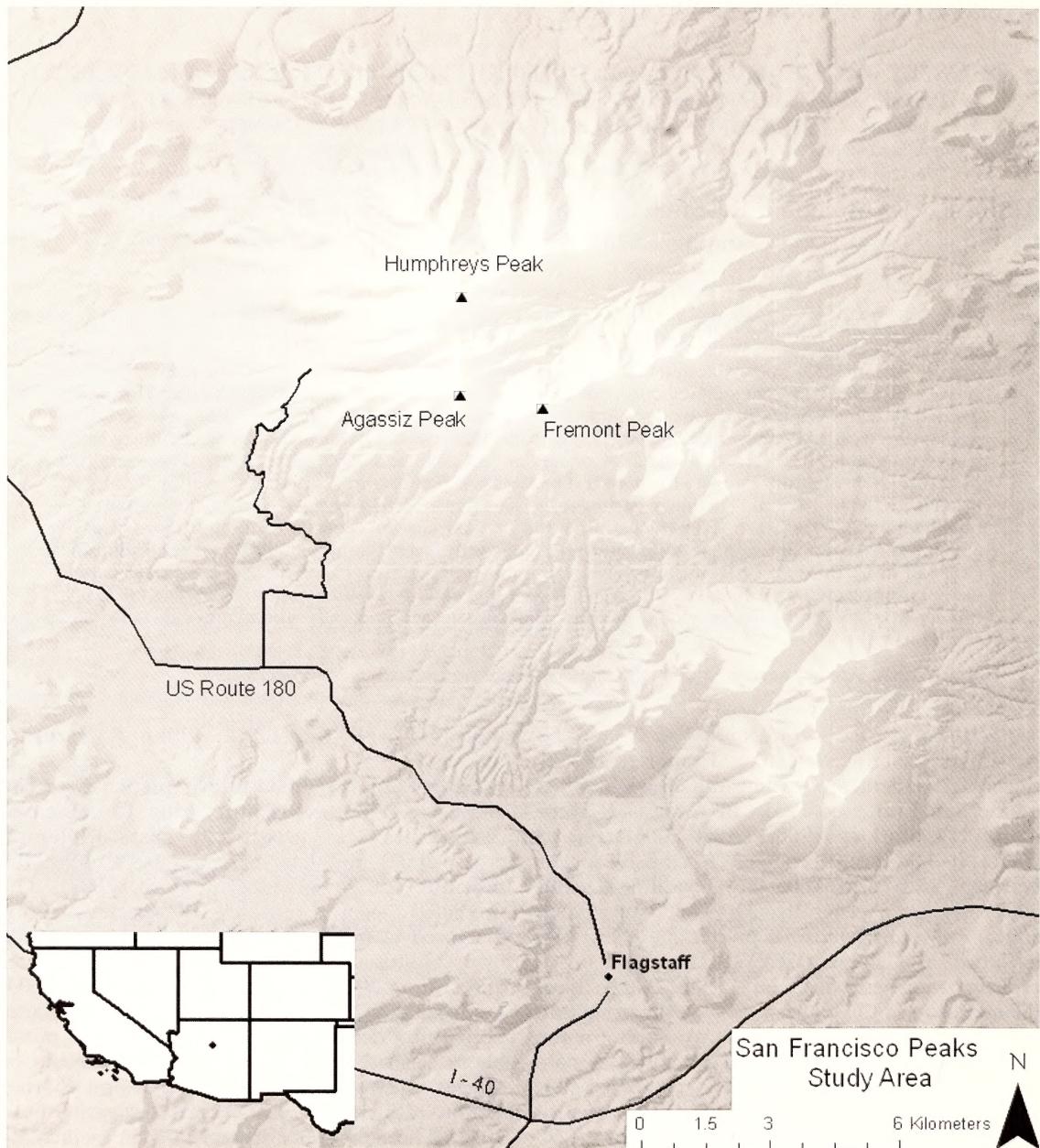


FIG. 1. *Packera franciscana* study area showing the San Francisco Peaks in northern Arizona with the inner basin in an extended volcanic caldera to the northeast. Humphreys Peak is at $35^{\circ}20'45.781''N$; $111^{\circ}40'40.102''W$; and 3854 m elevation.

dance do not exist. Yet, such data are critical for recovery of the species under the Endangered Species Act from either recreational impacts or future climate change. Off trail use of above treeline habitats on the San Francisco Peaks is currently banned due to concerns about potential negative impacts on *P. franciscana*. Our study defines baseline population densities along permanent transects under current climate and recreational use conditions which therefore may

allow the detection of future population trends. Specifically, our objectives are to: 1) establish a statistically robust sampling protocol for long-term population density trends; 2) determine the elevation of patch centroids along these transects to allow early detection of climate change driven altitudinal migration; and 3) provide data for species assessments, management responses, and revision of the 23-year old Species Recovery Plan (Phillips and Phillips 1987).

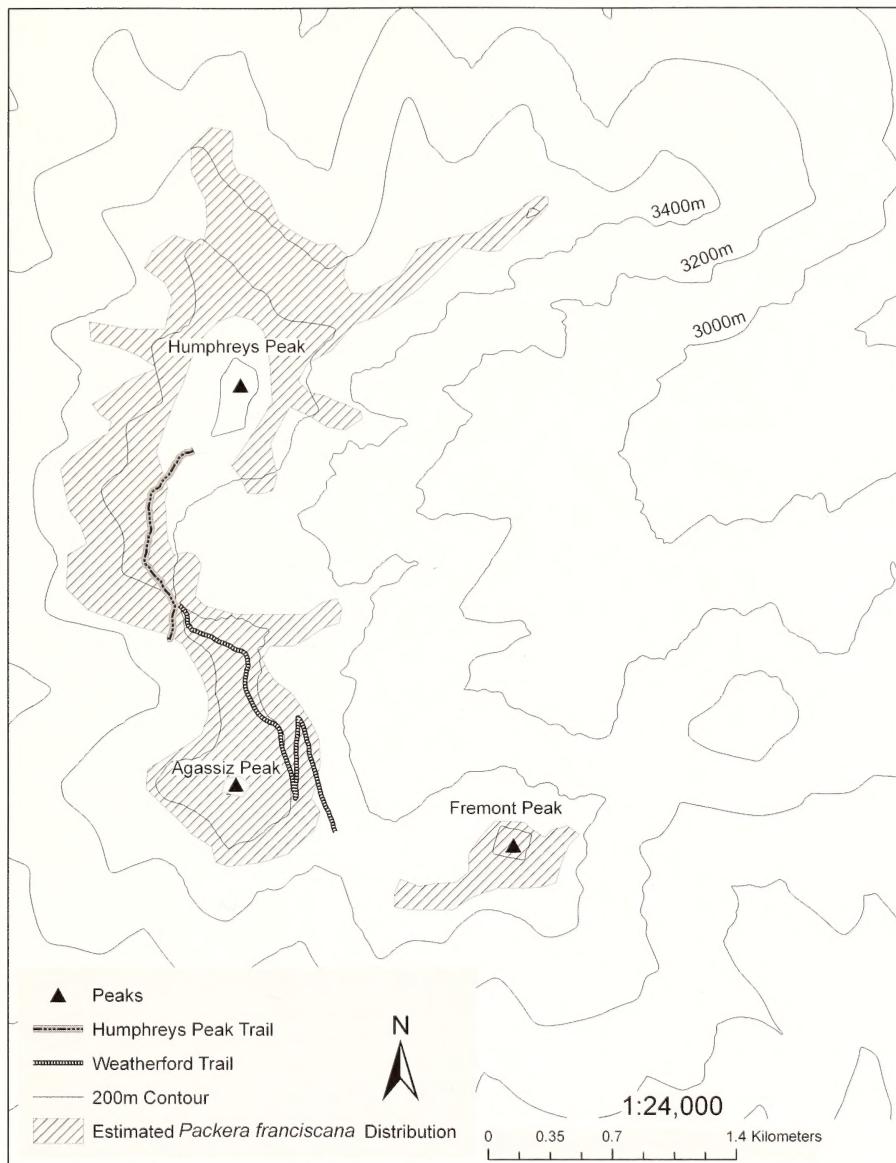


FIG. 2. Site map showing the approximate distribution of *Packera franciscana* and the location of sampling transects along recreational trails on the San Francisco Peaks. The Humphreys Peak Trail transect is on the outer volcanic slopes through and above treeline, and the Weatherford Trail transect is mostly within the inner caldera basin but crosses to the outer slopes near its junction with the Humphreys Peak Trail. Distribution map was modified from Dexter (2007) to group his polygons and include areas where we found *P. franciscana*. *Packera franciscana* was not found at the top of Humphreys or Agassiz Peaks but was found at the top of Fremont Peak.

METHODS

In 2008 we established an elevational transect along the Humphreys Peak Trail on outer slopes of the San Francisco Peaks through *P. franciscana* habitat to estimate the density of *P. franciscana* ramets, mid-September flowering/fruiting phenology, and the population centroid elevation as the population intersects the trail (Fig. 2). Fifty seven sample points were established at 25 m intervals along a transect starting

at 3520 m elevation, below the first *P. franciscana* occurrence, and extending 1425 m along the trail to an elevation of 3798 m which is above the last trail-side occurrence. In mid-September 2008 and 2009 after the monsoon season, we counted *P. franciscana* ramets (upright stems) within 12 individual 1 m² frames at each sample point arranged along the trail edge to allow flexibility for trail curvature (Fig. 3). Ramet counts were chosen as an estimate of abundance since *P. franciscana* is a rhizomatous species (Barkley



FIG. 3. Sampling frame layout along the Humphreys Peak and Weatherford Trails transect showing the 0–1 m and 1–2 m bands. Both layouts had 12 sampling frames per sample point.

1968; Trock 2006). Sampling frames were omitted when they overlapped previously counted frames along trail switchbacks, covered recent trail maintenance areas, or covered vertical drop-offs >5 m. Counts of ramets with flower, fruit, or both were also made within each frame. In September 2009 we added an inner basin transect along the Weatherford Trail (Fig. 2) to increase sample size and habitat diversity. This hiking trail runs mostly within the San Francisco Peaks volcanic caldera and crosses a large talus slope. This transect began at 3449 m, below where the first *P. franciscana* plants were noted, and continued with 110 sample points at 25 m intervals along the trail to its junction with the first trail at 3569 m. Sampling intensity, 12 frames per sample point, was the same as that on the first trail but arrangement of the sampling frames was restricted to within one meter of the trail edge due to the large amounts of loose talus off trail (Fig. 3). Coordinates for latitude, longitude, and elevation were made for each sample point with a Trimble® Geo XT 2005 Series GPS (Trimble Navigation Ltd, Sunnyvale, CA) with sub-meter accuracy to allow relocation of each sample point in subsequent years.

Descriptive and inferential statistics were calculated with SAS/STAT 9.2 (SAS Institute

Inc, Cary, NC). Population centroid elevations were calculated in Proc Means as the elevation of each sample point weighted by the number of ramets, so that each ramet received equal weight. Proc GLIMMIX with a negative binomial distribution function was used to test for type III fixed effects differences in ramet count between years and trail-side bands (distance from trail; 0–1 m vs. 1–2 m). Proc GLIMMIX with a normal distribution function was used to test for differences in elevation of *P. franciscana* occurrences between the inner basin and outer slopes. The Standardized Morisita index of dispersion was calculated to measure ramet count aggregation (Krebs 1989).

RESULTS

Packera franciscana occurred from 3529 to 3722 m elevation within two meters of the Humphreys Peak Trail transect. Within its range of occurrence along the trail, densities within the two-meter bands along each side for 2008 and 2009 were 4.18 and 2.74 ramets m^{-2} , respectively (Table 1). There was no significant difference in overall ramet density between years ($F_{1, 0.05} = 0.45$, $P = 0.502$). There was also no significant difference in ramet density between the 0–1 m bands and the 1–2 m bands ($F_{1, 0.05} = 2.43$, $P = 0.123$) for either year ($F_{1, 0.05} = 0.34$, $P = 0.561$).

The elevation of the *P. franciscana* population centroid along the Humphreys Peak Trail, weighted by ramet density at each sample point, was 3640 (± 5 SE) m for 2008 and 3641 (± 7 SE) m in 2009 (Table 1). The overlapping standard errors indicate no significant change in elevation between years.

In 2009, we added transect sampling points for *P. franciscana* along the Weatherford Trail, using only the 0–1 m band due to the large amount of loose volcanic talus just off the trail. *Packera franciscana* was found along this trail from 3471 m elevation to its junction with the Humphreys Peak Trail, both on the inner basin side and the outer volcanic slopes. In September 2009 we counted 1315 ramets of *Packera franciscana* at 163 sample points along the two transects. Ramet counts per sampling frame ranged from 0 to 180 and reflected the species' visual patchiness. The Standardized Morisita index of dispersion ($I_p = 0.54$) indicates a clumped pattern of ramet counts since it is between 0 (random) and +1 (maximum aggregation). The elevation of the 2009 population centroid for both transects combined was at 3586 (± 10 SE) m (Table 1), but the inner basin centroid, 3547 m, was significantly lower than the outer slopes centroid, 3638 m ($F_{(0.05), 1, 28} = 14.92$, $P < 0.001$).

The overall *P. franciscana* 2009 trailside density estimate was 4.36 ramets m^{-2} within its

TABLE 1. ESTIMATES FOR DENSITY AND ELEVATION OF POPULATION CENTROIDS FOR *PACKERA FRANCISCANA* ON THE SAN FRANCISCO PEAKS IN NORTHERN ARIZONA. Density estimates follow a negative binomial distribution in which variance (var) is described by the negative binomial dispersion factor (k) and the square of the mean. The value of "k" given here was estimated by Proc GLIMMIX during statistical comparisons of the respective density estimates; variance in this table is the sample variance. Estimates for elevation of the population centroid are the mean of sample point elevations weighted by *P. franciscana* density which follow a normal distribution with standard errors (SE).

Sample location	Density ramets m^{-2}	var	n	k	Centroid elevation	SE
Humphreys Trail 2008	4.18	82.27	42	7.9	3640 m	± 5 m
0–1 m	2.02	31.65	42	9.7		
1–2 m	6.41	294.13	42	9.7		
Humphreys Trail 2009	2.74	44.58	42	7.9	3641 m	± 7 m
0–1 m	2.25	40.66	42	9.7		
1–2 m	3.31	71.82	42	9.7		
Inner basin 2009	5.62	143.86	77	9.6	3547 m	± 7 m
Outer volcanic slopes 2009	2.89	48.57	63	9.6	3638 m	± 7 m
Overall 2009	4.36	101.58	141	na	3586 m	± 10 m

elevational range of occurrence, 3471–3722 m on the San Francisco Peaks. The 2009 inner basin density was higher, 5.62 ramets m^{-2} , than the estimate for the outer slopes, 2.89 ramets m^{-2} but not significantly so ($F_{(0.05, 1,113)} = 2.82$, $P = 0.096$). The number of *P. franciscana* ramets within two meters of the Humphreys Peak Trail and within one meter of the Weatherford Trail is over 36,000 (density estimate * sampled length).

Phenological measurements for *P. franciscana* during our mid-September sampling period were similar for 2008 and 2009, with 9% of the ramets either flowering and/or fruiting in 2008 versus 6% in 2009. There was less than 1% difference between inner basin and outer slopes flowering/fruiting rate in 2009.

DISCUSSION

The Recovery Plan (Phillips and Phillips 1987) offers an overall estimate of 100,000+ clones of *P. franciscana* on the San Francisco Peaks as a general estimate of population size. Phillips and Peterson (1980) reported a *P. franciscana* population density range of 50–370 plants $100 m^{-2}$ on Agassiz Peak near the Weatherford Trail but did not clearly define plants as ramets or genets (clumps or clones) or describe estimation techniques. However, later references to clump size would indicate that they were using the genet concept. On a per $100 m^2$ basis, our density estimate (436) is somewhat larger than the upper end of their density range (50–370), which may reflect the different "plant" definitions. Given the difficulty of defining and counting clumps or clones in the field, ramets provide a more accurate way to assess population density. Even though ramet density may inflate the number of functional plants, it is an accurate reflection of photosynthetic and reproductive potential. Phillips and Peterson (1980) also reported that 13%

of the *P. franciscana* plants were adult (sexually reproducing) which is comparable to the 6–9% of ramets we sampled which were flowering and/or fruiting in 2008–2009. Our results are consistent with the above data from the 1980's and give no indication of changing populations trends. Although these trail-side transects do not represent randomly selected population transects, they may be the only viable option since *P. franciscana* can inhabit large talus slopes which are very difficult to sample without uprooting plants near and within the sampling frame. These transects do sample the range of occupied habitats and observed densities in the center of its distribution in the San Francisco Peaks (Fig. 2). Our results and the estimate of >36,000 *P. franciscana* ramets in <2% of its range would indicate that the species is locally abundant, persisting, and reproducing.

We interpret the successful production of fruit, which we observed actively dispersing by upslope winds in mid-September 2008, as an indication that *P. franciscana* can sexually reproduce on the San Francisco Peaks. Seed viability studies may provide additional support for this interpretation. Examination of plant root systems would be necessary to determine if new ramets originate from seed or from existing perennial rhizomatous clones. The hypothesis that rhizomes produce large patches of ramets is supported by the clumped pattern of ramet counts ($I_p = 0.54$). Although this may be the primary method of reproduction (USFWS 1983), we also found single isolated ramets during our sampling which could be the result of seed dispersal or rhizome fragments moving downslope in the talus substrate that *P. franciscana* inhabits. Plants inhabiting the upper portions of talus slopes would seem to be the result of seed dispersal since avalanches and downslope creep of talus fields would carry existing *P. franciscana* plants down-



FIG. 4. Photo of *Packera franciscana* (Greene) W.A. Weber and A. Löve herbarium specimen showing ramets from an extensive rhizome and adventitious root system.

slope. We noted dead *P. franciscana* plants at the base of some avalanche chutes. Our observations during voucher specimen collection indicate a relatively large root system comprised of rhizomes and adventitious roots that may not be attached to a stable substrate (Fig. 4). This growth habit in an unstable talus sea may be an evolutionary adaptation for survival and reproduction in that fragmentation of the rhizome by talus creep processes may be common. Thus *P. franciscana* may be well adapted to this type of disturbance.

The overall population centroid of 3586 m we measured is within the 3525–3605 m elevation range for most *P. franciscana* noted by Dexter (2007) and the 3350–3750 m main occurrence range in earlier reports (Phillips and Peterson 1980; U.S. Fish and Wildlife Service 1983). However, the population centroid for the out-slope samples located on a dry west-southwest slopes is 91 m higher in elevation than for the more east facing inner basin samples. The fact that southwest slopes have a higher *P. franciscana* patch centroid elevation lends credence to an upward migration hypothesis for this species in a future warmer drier climate.

We plan annual measurements of both transects to detect *P. franciscana* population trends. Sampling in subsequent years may indicate trends in population density, changes in September phenology, or elevational migration within its habitat. Changes in population density over time

may allow detection of climate change effects, population cycles, or recreational impacts. Changes in the elevation of population centroids or September phenology will more likely be the result of climate change.

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PLANT POPULATION AND HABITAT CHARACTERISTICS OF THE ENDEMIC SONORAN DESERT CACTUS *PENIOCEREUS STRIATUS* IN ORGAN PIPE CACTUS NATIONAL MONUMENT, ARIZONA

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ABSTRACT

Peniocereus striatus (Brandegee) Buxb. (Cactaceae) is an endemic Sonoran Desert cactus that reaches its northern range limit in southwestern Arizona. One U.S. population occupies a small area of Organ Pipe Cactus National Monument near the U.S./Mexico international boundary, which has been monitored since 1939. An extensive survey conducted in 2002, covering 177 ha, resulted in the discovery of 88 new plants, in addition to the relocation of 57 plants found in previous surveys. Despite potential increases in population size and spatial distribution, mean plant height and number of basal stems has not significantly changed in recent years. Bud scars revealed that a majority of the population was sexually mature. *Peniocereus striatus* occurrence increased with decreasing slope, spanned every slope aspect, and was highest on rocky soils, but was noticeably low on west and northwest slopes and areas where severe land degradation had previously occurred. Over half of *P. striatus* plants were nursed by shrubs and subshrubs, while 40% occurred under leguminous trees. A severe frost in January 2002 top-killed 19% of the population, with the greatest damage in drainage bottoms. However, long-term (1944–2002) climate records show that there has been an overall increase in the number of frost free days in the region, which, coupled with land use change, has implications for the future health of this population.

Key Words: Cardoncillo, climate, frost-tolerance, gearstem cactus, habitat suitability, land use history, night-blooming cereus, nurse plant.

The small population sizes, narrow geographic ranges, and high habitat specificity make rare endemic plant species particularly vulnerable to accelerated climate and land use changes (Rabinowitz 1981; Malcolm et al. 2006). The viability and persistence of rare endemic plants depends on the maintenance of suitable habitat and the ability of the population to propagate itself under changing environmental conditions. In the Sonoran Desert, several endemic plants, including cacti, are of tropical descent and known to be limited in their northern distribution by freezing temperatures (Shreve 1911; Hastings 1963). Anthropogenic global warming is likely to decrease the intensity and frequency of freezing temperatures, which may create opportunity for expansion of frost-intolerant plant species (Lyford et al. 2003). In addition to climate, Sonoran Desert endemic plants are likely to respond to changes in land use that occur in their local

habitat, including livestock grazing, wood harvesting, cropping practices, and other activities (Suzán et al. 1994). Close study and monitoring of plant populations and their habitat at the periphery of their geographic ranges can contribute to an understanding of the factors that limit their distribution, provide information on the sustainability of the population, and help inform conservation strategies.

Peniocereus striatus (Brandegee) Buxb. is a slender-stemmed cactus endemic to frost-free areas of the Sonoran Desert (Felger 2000). This inconspicuous sub-erect to sprawling, vine-like cactus is typically 25–75 cm tall (Pinkava 1995) and up to 2 m tall in some microhabitats (Felger 2000). *Peniocereus striatus* has small, scattered populations throughout Mexico (Baja California, Sonora, and Sinaloa) and is very rare in the U.S., where it reaches its northern range limit in southwestern Arizona (Benson 1982; Nabhan 1992; and Felger 2000). One of the few *P. striatus* populations in the U.S. occurs in a small area of Organ Pipe Cactus National Monument

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(OPCNM) near the U.S./Mexico international boundary. This population was first recorded from Gray's Well in 1939 (OPCNM Herbarium, NE of Sonoyta, 20 April 1939, A.A. Nichol s.n.), and no other population has been reported from any other area in OPCNM.

Past research has found that populations of *P. striatus* have higher densities and larger plant sizes south of OPCNM at less disturbed sites (Suzán et al. 1994). The condition of *P. striatus* improves under perennial nurse plants, which modify the environment by buffering extreme temperatures, increasing water and nitrogen availability, reducing photosynthetically active radiation, providing physical support and protection from herbivores (Franco and Nobel 1989; Suzán et al. 1996). Recruitment of *P. striatus* is low, most likely because it has few species of pollinators, blooms nocturnally during a few episodes, and has low floral and fruit production (Benson 1950; Suzán et al. 1994; Raguso et al. 2003).

Previous reports suggested that *P. striatus* in OPCNM occurred more frequently on rocky hill slope habitat (Jackson 1966; Steenbergh 1966; Suzán et al. 1994; Goodsell unpublished), which contrasts with observations that *P. striatus* in Mexico prefers flat sites more than rocky slopes (T. Van Devender and M. Dimmitt, Arizona-Sonora Desert Museum, personal communication; G. Anderson and S. Rutman personal observation). We hypothesize that *P. striatus* occurred on rocky hill slopes in OPCNM during a historical period of high land use intensity because these sites provided refugia from plant mortality and habitat degradation associated with livestock grazing and other land management practices. We predict that the population of *P. striatus* in OPCNM has expanded from the area occupied during the original survey for two main reasons. First, deleterious management practices have ceased, potentially allowing for increased recruitment, germination, and survival of *P. striatus* plants, as well as the regeneration of *P. striatus* nurse plants, which create suitable habitat for growth. Second, the frequency and duration of freezing temperatures in the winter has likely decreased since the population was first recorded. As winter freezing temperatures decrease, the survival and reproduction of these frost-intolerant plants might increase.

In this study, we use over 60 years of monitoring results to determine the population and habitat characteristics of *P. striatus* in OPCNM and provide some evidence of how climate and land use changes can affect succulent plants at the limits of their distributions. Our specific objectives were to: 1) determine the size, spatial distribution, and reproductive capacity of the population; 2) identify suitable habitat characteristics, including the use of nurse plants;

and 3) assess past and current climate and land use threats to the population.

METHODS

Site Description

Organ Pipe Cactus National Monument is an International Biosphere Reserve located in southwestern Arizona, 210 km W of Tucson and 35 km S of Why, AZ (31.82–32.20°N, 112.61–113.09°W). Organ Pipe Cactus National Monument includes several high mountain ranges and low basins, with elevations ranging from 300–1470 m. Long-term (1944–2002) mean annual temperature at low elevation is 21.0°C (mean min. = 12.1°C, mean max. = 29.9°C) and mean annual precipitation (MAP) is 238 mm. Precipitation at OPCNM is bimodally distributed, with nearly half of the precipitation delivered during winter (October–March) storms and the remainder during the summer monsoon (July–September). April–June are extremely dry, with total precipitation in these months composing 4% of MAP.

Organ Pipe Cactus National Monument was established in 1937 to protect the organ pipe cactus (*Stenocereus thurberi* (Engelm.) Buxb.) and the Sonoran Desert ecosystem. The OPCNM *Peniocereus striatus* population occurs within a *Larrea tridentata*-*Ambrosia deltoidea* association on floodplains and lower bajadas, an *Atriplex polycarpa*-*A. linearis* association on loamy floodplains, and a *Prosopis velutina*-*Parkinsonia microphylla*-*Olneya tesota* association on hill slopes.

Monitoring History of the *P. striatus* Population in OPCNM

Thirty years following the first documentation of *P. striatus* in OPCNM in 1939, the National Park Service (NPS) reported the species was rare and occurred only on north- and east-facing hill slopes (Jackson 1966; Steenbergh 1966). In 1969, the (NPS) surveyed in the proximity of the original location and reported a total population of 36 plants on three hills (Goodsell unpublished). As part of the Sensitive Ecosystem Program in OPCNM, probable habitat, defined as hill slopes in the vicinity of the plants found in 1969, was surveyed for *P. striatus* in 1990. The survey resulted in the location of 59 plants (11 plants per ha in suitable habitat), which produced an estimate of the extant population in OPCNM of less than two hundred individuals (Johnson et al. 1990; Ruffner and Associates 1995). As a result of this survey, the NPS measured the height and survivorship of 22 *P. striatus* plants from 1991–1996. Another survey occurred in 1994, when 47 plants in OPCNM were located and tagged for a

study on the pollination ecology of *P. striatus* (Nabhan and Suzán 1994). Some of these individuals were relocated in 1999, when volunteers surveyed the eastern portion of its range in OPCNM. Fifty-seven plants were found, tagged and mapped. About two dozen *P. striatus* plants were tagged in 1991 and revisited from 1993–1999 to determine population characteristics (Ruffner and Associates 1995), with little to no information recorded about habitat requirements.

2002 Survey

To determine the population size, distribution, and habitat preferences of *P. striatus* in OPCNM, a systematic survey was conducted from January–July 2002. Most of the survey was performed by a single person trained in the appearance and growth habits of the plant. Survey intensity ranged from belt transects (5–10 m wide) in low density vegetation to more intensive surveys in xeroriparian areas. All open areas and every nurse plant species was checked for the presence of *P. striatus*. The survey was initiated in previously occupied habitat determined by previous NPS reports (Jackson 1966; Steenbergh 1966; Goodsell unpublished) and expanded into potential habitat until the survey no longer located plants or the international boundary was encountered. Survey tracks were recorded with a high precision GPS unit (accuracy ~3 m), and survey area was created by buffering survey tracks in a GIS.

The location and elevation of *P. striatus* plants were also recorded using a high precision GPS unit. Plants were marked with numbered metal tags and the maximum height and width of each plant, as well as the number of live and dead basal stems per plant were recorded. Height and width measurements were taken during winter dormancy and only green succulent stems of plants were measured. To determine herbivory damage, the presence or absence of injury to a plant and proximity to a rodent hole were recorded. Since flower bud scars are obvious and persist for a long time, they were used to indicate reproductive status. The nurse plant (*sensu* Franco and Nobel 1989) and its spatial orientation to *P. striatus*, as well the nearest perennial plant neighbor and its distance to *P. striatus* were noted.

Slope, aspect and other descriptors of the physical environment were recorded. Soil surveys from OPCNM (USDA–Soil Conservation Service 1972) were used to produce a digital data layer of soil types within the *P. striatus* survey area. Lastly, whether or not the plant was within two meters of an ephemeral drainage was observed and recorded.

Climate and Land Use History

Precipitation was measured at the Dos Lomitas rain gauge, located within the study area, and temperature was measured at the National Weather Service station located at park headquarters 20 km NW of Dos Lomitas. To assess past land use history of the study area, a map of historic land use was prepared. A digital ortho-photo quadrangle, formed from a 1997 photographic image, was used as a base layer onto which lines and polygons were drawn to indicate roads, corrals, wells, historic agricultural fields and disturbance zones. Early aerial photographs of the area were compared with the 1997 ortho-photo quad to verify or interpret linear features and other patterns of land use. Some man-made features found on the ortho-photo quad were verified on the ground using GPS. Archived documents at OPCNM provided additional information on past land management activities (Rutman 1996).

Statistical Analyses

The height and width of *P. striatus* in 2002 were broken into 10 cm size classes to assess population structure. Changes in height and number of basal stems through time were evaluated using repeated measures ANOVA (R Development Core Team 2008). The proportion of the total population in each slope class, aspect, soil type, nurse plant, and nearest perennial plant was determined. Pearson's Chi-square tests were performed to determine if observed occurrences were different than an expected random distribution in potential habitat. ANOVA was also performed on height of *P. striatus* to see if there were differences among nurse plant associations. A linear regression model was fit to determine trends in temperature through time.

RESULTS AND DISCUSSION

Population Characteristics

A survey of 172 ha of potential *Peniocereus striatus* habitat in OPCNM resulted in the discovery of 88 new plants, in addition to the relocation of 57 plants found in the 1999 survey, which makes the density of the population 0.85 individuals per ha. This population size of 145 plants is larger and population density two orders of magnitude greater than estimates reported by Suzán et al. (1994). The close proximity (<3 m) of many new *P. striatus* found in the 2002 survey to those found in 1969 (Fig. 1), and the discovery of small individuals in 2002, provide further evidence that there have likely been increases in the population size. The population also appears to have expanded from its restricted spatial

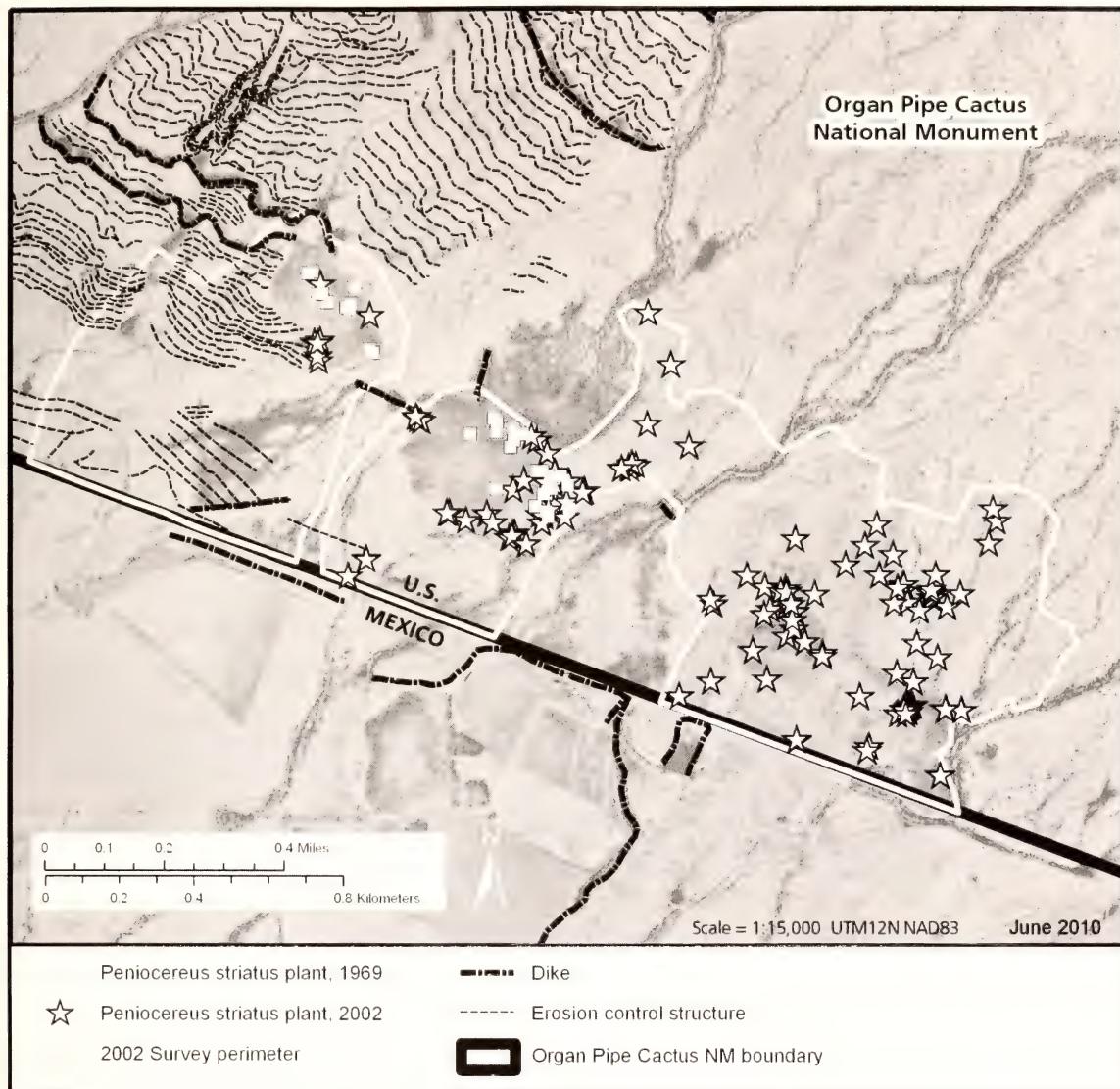


FIG. 1. Location of *Peniocereus striatus* individuals from 1969 and 2002 surveys and land use disturbances in Organ Pipe Cactus National Monument.

distribution on hillslopes in 1969 to adjacent low-lying areas, but individuals were notably absent from the farthest western portion of the survey area where intense land use modification had occurred (Fig. 1). Potential increases in population size and spatial distribution may be partially due to differences in survey efforts, which were not well described in historic records.

The mean height of plants in 1993 did not significantly change in subsequent surveys in 1994–2002 (Fig. 2a). The mean number of basal stems did not significantly change from 1999 to 2002, although there was a trend for stem number to increase (Fig. 2b). The mean height and width of plants were 58.6 cm (± 2.5 cm standard error) and 54.4 cm (± 3.7 cm), respectively. The height

distribution of the population ranged from 1 to 158 cm and had a significant (>2 standard errors of skewness) positive skew (1.02), which means the tail of the distribution was shifted towards taller individuals (Fig. 3a). While a majority of individuals in the *P. striatus* population were 40–80 cm tall, it is likely that the interaction *P. striatus* had with nurse plants allowed for the growth of tall individuals by facilitating an environment that was favorable for plant growth. The tallest plant of 158 cm was close to the maximum recorded height of 200 cm (Felger 2000; Goodsell unpublished). The horizontal width distribution was bimodal, with most individuals <10 cm or 30–70 cm (Fig. 3b). This reflects the vine-like (narrow) and bush type

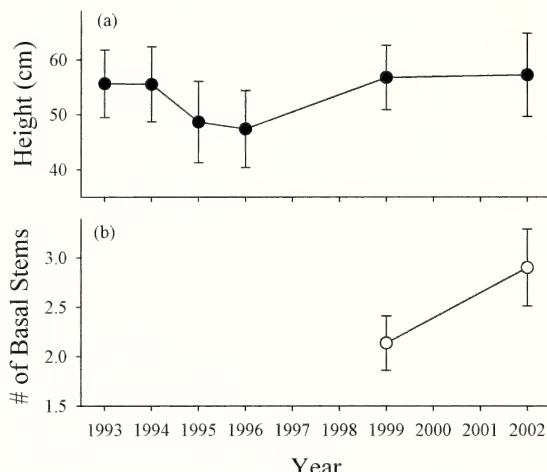


FIG. 2. Mean height (a; $n = 15$) and total number of basal stems per plant (b; $n = 51$) of *Peniocereus striatus* from 1993–2002. No significant differences among years ($P > 0.05$).

(wide) morphological types first described by Johnson et al. (1990). The vine-like morphs often occurred under trees and had long branches that draped across nurse plant stems, while the bush-type morphs appeared to have shorter, more erect branches and usually grew within the canopies of shrubs and subshrubs or in the open. The maximum width of 304 cm exceeded previously reported values (Johnson et al. 1990; Pinkava 1995; Anderson 2002). Most plants had a single living basal stem, although at least one plant had eight stems.

A majority of *P. striatus* individuals in the OPCNM population were sexually mature. The presence of bud scars indicated that 76% of the plants had flowered in the past. For the remainder of the population, reproductive status could not be determined, either due to herbivory or aboveground tissue damage. In July 2002, 45% of *P. striatus* individuals had buds present, including two plants that lacked bud scars from prior reproductive activity.

Habitat

Peniocereus striatus occurred at a low, fairly narrow elevation range between 388–441 m, which is within the elevation range of 60–450 m reported for this species (Benson 1982). The number of plants decreased with increasing slope: 35% of plants occurred on <2% slope, while only 5% of plants occurred on >22% slope (Table 1). This suggests that there has been expansion of the population from its restricted historical hill slope habitat. *Peniocereus striatus* occurred on every slope aspect, but had a tendency to occur less frequently on west and northwest facing slopes ($\chi^2 = 21.5$, $P = 0.003$,

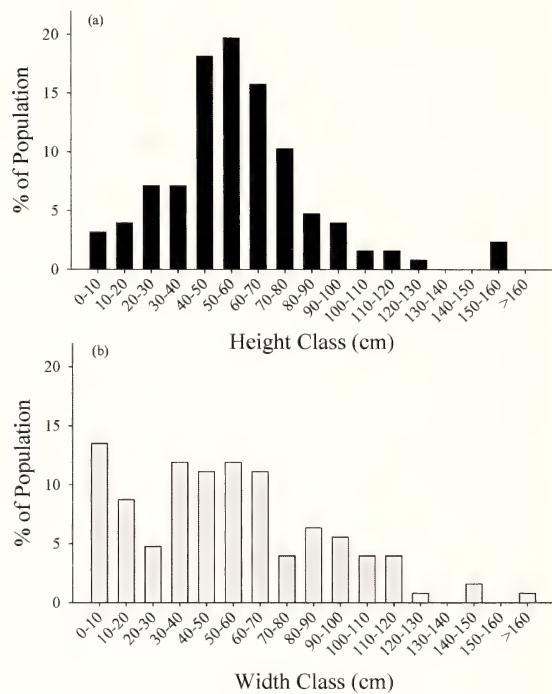


FIG. 3. Percent of the *Peniocereus striatus* population in height (a) and width (b) classes. Height distribution skewness = 1.024, kurtosis = -0.375. Skewness and kurtosis is considered significant if greater than 2 standard errors of normal distribution = ± 0.436 .

$df = 7$; Fig. 4a). This result is consistent with earlier reports that suggested *P. striatus* occurred less frequently on west-facing slopes (Steenbergh 1966; Goodsell unpublished). While many cacti in OPCNM attain their greatest densities on south-facing slopes since they are less subject to freezing temperatures in the winter (Parker 1987), the current *P. striatus* distribution is not limited to these slopes, perhaps because they are frequently buffered from extreme environmental conditions by nurse plants.

Peniocereus striatus occurred on five different soils and three landform types within the 2002 survey area (Table 1). Plants occurred less frequently on fine and very fine sandy loams and more frequently on rocky soils than predicted if plants were randomly distributed in their potential habitat ($\chi^2 = 109.4$, $P < 0.0001$, $df = 5$). Twenty-seven percent of the population occurred on deep, very fine or fine sandy loam on gently sloping floodplains, nearly half of the plants occurred on very gravelly or cobbly loam on dissected alluvial fans, and another quarter of the plants grew on very stony loam on hill slopes (Table 1). *Peniocereus striatus* was not found on torrifluvents of the drainage bottoms, although this substrate type only represented 4.3 percent of the survey area. Although these results are consistent with historical accounts of greater *P.*

TABLE 1. HABITAT CHARACTERISTICS OF *PENIOCEREUS STRIATUS* POPULATION AT ORGAN PIPE CACTUS NATIONAL MONUMENT.

Habitat	% of population
Slope	
0–2%	35
3–8%	25
9–14%	21
15–21%	14
>22%	5
Soil type	
Gunsight very gravelly loam	41
Gilman very fine sandy loam	26
Lomitas very stony loam	24
Harqua very cobbly loam	8
Antho fine sandy loam	1
Torrifluvents	0

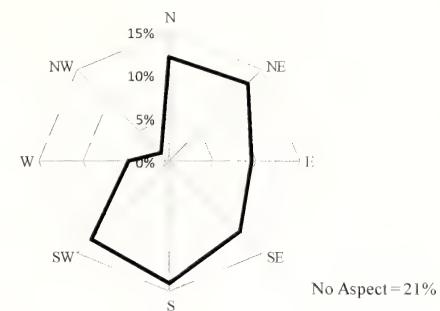
striatus occurrence on rocky soils, the population has expanded to other soil types.

Nurse Plant Associations

Most *P. striatus* plants in OPCNM grew within the canopy of subshrubs, shrubs and trees. Nabhan and Suzán (1994) also found that *P. striatus* was non-randomly distributed in the environment, preferring microsites under nurse plants to microsites with no plant cover. Over half of *P. striatus* plants were nursed by shrubs and subshrubs, while 40% occurred under leguminous trees (Table 2). These results are similar to Nabhan and Suzán (1994), who found that 50% of *P. striatus* grew under trees. A majority of *P. striatus* that had nurse plants were directly within them, while most others were oriented either directly north or south of the nurse plant ($\chi^2 = 47.0$, $P < 0.0001$, $df = 7$; Fig. 4b). An orientation north of the nurse plant can be explained by protection against excessive radiation, temperature, and water stress (Franco and Nobel 1989), while an orientation south of the nurse plant may provide protection against frost (Suzán 1994).

While we found *Prosopis velutina* Wooton to be the most commonly used nurse plant by *P. striatus*, Nabhan and Suzán (1994) reported *Olneya tesota* A. Gray was the species' principal nurse plant. Besides providing shade and physical protection, legume trees also increase soil nitrogen levels under their canopies (Franco and Nobel 1989). Johnson et al. (1990) observed that *Ambrosia deltoidea* (Torr.) W. W. Payne, *Larrea tridentata* (DC.) Coville, and *Parkinsonia microphylla* Torr. were the most common nurse plants for *P. striatus*. The earliest report of the OPCNM population mentions *Larrea tridentata* as the most common associate (Goodsell unpublished), followed in quantity by plants standing entirely alone. Nurse plant type significantly affected the

(a)



(b)

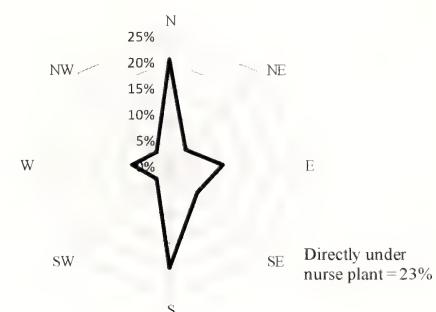


FIG. 4. Percent of the *Peniocereus striatus* population on each aspect (a) and orientation in relationship to nurse plant (b). Aspect: $\chi^2 = 21.4$, $P = 0.003$, $df = 7$, orientation to nurse plant: $\chi^2 = 50.2$, $P < 0.0001$, $df = 7$. Chi-square test assumes expected population is evenly distributed in each direction.

mean height of *P. striatus*. Plants underneath trees were significantly taller than those under subshrubs, while plants underneath shrubs and those with no nurse plant association had an

TABLE 2. NURSE PLANT ASSOCIATIONS OF *PENIOCEREUS STRIATUS* POPULATION AT ORGAN PIPE CACTUS NATIONAL MONUMENT.

Nurse plants	% of population
Subshrubs	25
<i>Atriplex linearis</i> S. Watson	13
<i>Ambrosia deltoidea</i> (Torr.) W. W. Payne	12
Shrubs	29
<i>Larrea tridentata</i> (DC.) Coville	14
<i>Atriplex polycarpa</i> (Torr.) S. Watson	11
<i>Lycium</i> spp.	4
Trees	40
<i>Prosopis velutina</i> Wooton	21
<i>Parkinsonia microphylla</i> Torr.	12
<i>Olneya tesota</i> A. Gray	7
Other	6
None	4
<i>Prosopis velutina</i> (dead)	1
Unknown shrub (dead)	1

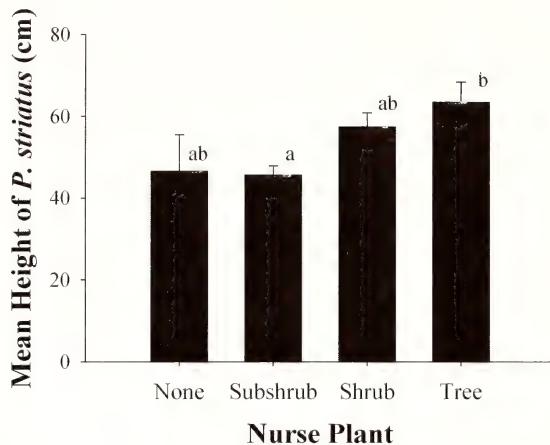


FIG. 5. Mean height of *Peniocereus striatus* in relationship to the nurse plant type (none, subshrub, shrub, tree). Different letters designate significant differences (Tukey adjusted $P < 0.05$).

intermediate height (Fig. 5). This supports our hypothesis that *P. striatus* makes opportunistic use of the structural support of the available perennial canopy and that the shrubby morph is more likely to be found in the open or under a subshrub. *Peniocereus striatus* was on average $16.7 (\pm 1.7)$ cm from the nearest perennial plant, which was most commonly a subshrub (55%), either *Ambrosia deltoidea* or *Atriplex linearis* S. Watson, followed in close proximity to shrubs (30%).

Threats to Population

Climate. Most plants had at least one dead basal stem, indicating that aboveground tissue

damage was widespread and common. During the winter-spring survey of 2002, 19% of *P. striatus* individuals with at least one previously green stem had all their stems become light brown, dry and brittle. Since most of the plant's biomass is belowground in diffuse tubercles (Benson 1982), this "top-kill" does not necessarily equate to plant mortality. One likely explanation for this observed "top-kill" is freezing temperatures. Temperature at the site dropped to -13.7°C on January 31, 2002, which is low enough to cause tissue damage or death of temperature-sensitive succulents (Nobel 1988). Position on the landscape significantly affected the probability of the 2002 aboveground tissue damage ($\chi^2 = 70.4$, $P < 0.0001$, $df = 3$): 36% of individuals that occurred ≤ 2 m from a drainage showed top-kill damage while only 8% of individuals > 2 m from a drainage were damaged. Since drainages are frequently affected by cold nocturnal air inversions due to radiative cooling and cold air flow from sidewalls (Brunt 1939), the higher incidence of top-kill in low-lying areas was likely caused by low temperatures. By early summer 2002, more than half of top-killed plants had re-sprouted from the base or had new branches growing from the desiccated stems.

The likelihood of frost damage is likely to decrease in the future as temperatures warm due to anthropogenic greenhouse gas emissions. Over the last fifty years (1949–2002), the number of freezing days has declined from greater than 20 to less than 10 days per year (linear regression: slope = -0.33 , $r^2 = 0.41$, $P < 0.0001$; Fig. 6), the average minimum January (coldest month in OPCNM) temperature has increased 2.3°C , and this average has not been below freezing since

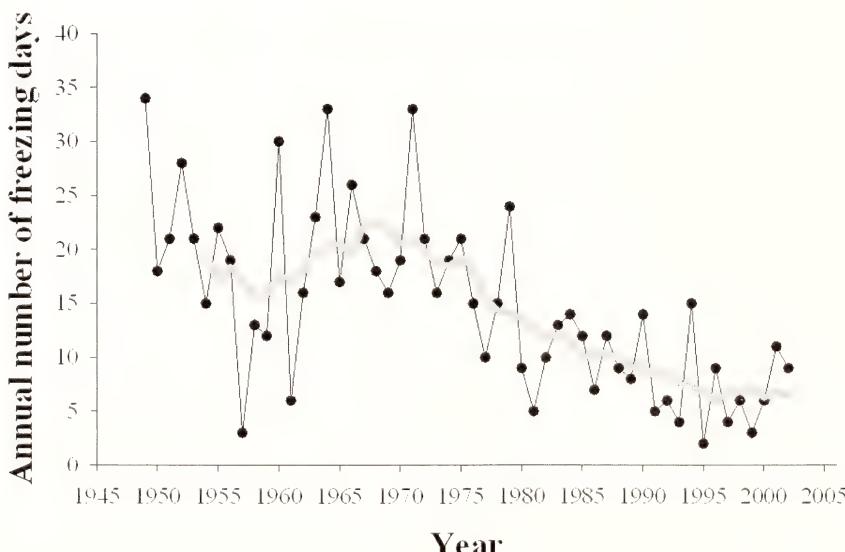


FIG. 6. Annual number of freezing days at study site from 1949–2002 (black line) and 10-year moving average (gray line). Linear regression: slope = -0.33 , $r^2 = 0.41$, $P < 0.0001$.

1949 (not shown). Given that minimum temperatures likely limit the range of *P. striatus*, these changes in temperature may explain potential increases in the *P. striatus* population. Future increases in temperature are likely to result in the spread of frost-intolerant succulents and other plants northwards in their distribution.

Herbivory. Most *P. striatus* plants (70% of the population) displayed signs of herbivore damage during the winter 2002 survey, likely caused by rodents and lagomorphs. In 2002, 17% of new stems initiated in the spring showed signs of herbivory by July. Nearly half (45%) of the total population was within 1 m of a rodent hole, which suggests a high animal density in close proximity to the cactus population.

Land use. The habitat of *P. striatus* is located in an area of OPCNM heavily degraded by past land use and land management practices. Concentrated livestock grazing, wood harvesting, and farming were among the land use activities within the study site at the Gray Ranch headquarters (Rutman 1996). The overstocking of cattle had adverse environmental effects, including damage to *P. striatus* and its habitat, which continued until livestock were removed in the late 1970's (BLM 1966; Schultz et al. 1971). On certain soil types in the study area, poor livestock grazing practices led to accelerated erosion, expressed as deeply entrenched channels and headcuts that moved upstream as much as 8 m per rainstorm in 1952 (OPCNM historic photo, accession #1629). Large stumps and re-sprouted stems at the study site are signs of historic tree harvesting, while more recently, illegal woodcutters have taken tree branches using machetes (Nabhan and Suzán 1994). *Peniocereus striatus* could not have been present on a 13 acre flood-irrigated field used by the Gray family at the north end of the study area. Small diversion dams and retention dikes used to manage irrigation, which date back to the early 1930's, change water surface flows on several hundred acres of suitable habitat for *P. striatus*.

Potential habitat in the study area has also been disrupted by erosion control structures installed by the NPS and Soil Conservation Service in the 1950's–1960's. More than 50 years after their construction, these structures remained clearly visible in aerial photography (northwest corner of Fig. 1). Despite these structures, erosion rates have not slowed since 1977 (T. Marsh, unpublished data, 1977–1996). The loss of soil has undoubtedly had consequences for the local *P. striatus* population, as the roots would have been exposed or buried, depending on landscape position. *Peniocereus striatus* has not been found in or adjacent to these erosion control structures, which suggests that the species may be sensitive to the local watershed modifications caused by these structures.

Previous surveys and knowledge about the study area's land use history provides some evidence that the *P. striatus* population was historically restricted to rocky hill slope habitat, as reported by early surveyors. This landscape position was largely left undisturbed by livestock grazing, erosion, agriculture, and watershed modifications, which were concentrated on the low-lying and flatter portions of the landscape. The cessation of livestock grazing, coupled with warmer temperatures, may have allowed for the expansion of *P. striatus* into areas of the landscape where it was previously not found. Erosion control structures and their long-term effect on hydrology continue to exclude this species from otherwise suitable habitat.

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STAND DEVELOPMENT ON A 127-YR CHRONOSEQUENCE OF NATURALLY REGENERATING *SEQUOIA SEMPERVIRENS* (TAXODIACEAE) FORESTS

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ABSTRACT

Understanding the natural patterns of regeneration following human disturbance is essential for effective restoration and management of second-growth forests. Despite their unique ecological character, little is known about these patterns in *Sequoia sempervirens* (D. Don) Endl. (Coast Redwood) forests. We examined the composition and structure of naturally regenerating stands with 360 randomly located sample plots across a chronosequence of five replicated age-classes (18 to 127 yr) and three old-growth reference sites. Results indicate a progression of stand characteristics towards old-growth conditions, with several measures reaching old-growth equivalence within the timeframe of the chronosequence. Stand density, canopy cover, and species richness reached old-growth equivalence within 41–80 yr; Shannon-diversity reached old-growth equivalence between 80–100 yr; and the density of redwood seedlings and shrub cover reached old-growth equivalence between 100–130 yr. Basal area, herb cover, and the relative dominance of *S. sempervirens* progressed toward, but did not reach, old-growth equivalence. Size-class analysis indicated an increase in the density of large diameter trees, with no change in the density of smaller size-classes after forty yr. Coast redwood associated understory species were favored on the older sites with the cover of *Calypso bulbosa* (L.) Oakes, *Trillium ovatum* Pursh, and *Viola sempervirens* Greene reaching old-growth equivalence, while *Iris douglasiana* Herb., *Tiarella trifolia* L., and *Achlys triphylla* (Sm.) DC. did not. No non-native species were recorded in stands older than 60 yr. We conclude that coast redwood forests are resilient to human disturbance, though some old-growth characteristics may require more than a century to develop.

Key Words: Chronosequence, coast redwood, natural regeneration, second-growth, *Sequoia sempervirens*.

The coast redwood forest, dominated by *Sequoia sempervirens* (D. Don) Endl., is known for its high productivity, large carbon storage potential, and impressive stature (Preston 2007). Historically, *S. sempervirens* forests covered more than 8100 km² along the fog-shrouded coast from central California to southern Oregon. Due in large part to its value as a timber species, more than 95 percent of the original old-growth coast redwood forest has been converted into managed timber stands and other land uses (Noss 2000). With the majority of this forest type currently in second-growth, analysis of the natural patterns of stand development following timber-harvest is essential for effective management and restoration.

The dynamics of post-harvest development for *S. sempervirens* stands are unique among coniferous forests. *Sequoia sempervirens* possesses a natural resilience to disturbance due in part to its prolific vegetative sprouting ability (McBride 1977; Espinosa-Garcia and Langenheim 1991; Veirs 1996; Sawyer et al. 2000; Barbour et al. 2001). Though regeneration of *S. sempervirens* from seed can occasionally be abundant on mineral soils and fallen logs (Bingham and Sawyer 1988; Becking 1996; Porter 2002), the

majority of recruitment results from vegetative sprouts, especially following timber harvest (Douhovnikoff et al. 2004; Lorimer et al. 2009). The vascular connection between vegetative sprouts and existing root structures results in competition between stems for apical dominance, rather than for individual tree survival (Kauppi et al. 1987; Burrows 1990; Sachs et al. 1993; Laureysens et al. 2003). Issues of overcrowding that slow the regeneration of other coniferous trees do not affect *S. sempervirens* in the same manner. Instead, redundant clonal stems senesce over time, thinning the stand naturally without the risk of stand-scale mortality (Floyd et al. 2009; Lutz and Halpern 2006; Sach et al. 1993). Survival of suppressed trees is also unusually high for *S. sempervirens* as epicormic sprouting increases stem production when understory trees are released (Finney 1993).

Old-growth *S. sempervirens* forests are relatively stable in terms of composition and structure (Busing and Fujimori 2002) and follow a ‘gap phase’ regenerative pattern where suppressed understory trees expand to fill canopy gaps created by individual, or small group, blow-downs (Sawyer et al. 2000). Natural stand-replacing disturbance events are extremely rare

in *S. sempervirens* forests, even when compared to other coniferous forest types in the Pacific Northwest (Lorimer et al. 2009). As a result, the stand-scale removal of canopy through timber-harvest initiates regenerative patterns otherwise undocumented in this forest type.

Regeneration of *S. sempervirens* following timber harvest has been studied primarily in the context of post-harvest management practices such as planting, seeding, and thinning (Cole 1983; Oliver et al. 1994; Lindquist 2004a, b; Chittick and Keyes 2007; O'Hara et al. 2007). Very few studies have addressed the development of *S. sempervirens* stands in the absence of post-harvest management, and those that have been conducted focused on specific case studies or individual species rather than on forest regeneration as a whole (Boe 1965; Powers and Wiant 1970; Allen et al. 1996; Jules and Rathcke 1999).

Analysis of stand development of a long-lived species such as *S. sempervirens* (commonly exceeding 1500 yr in age) is best accomplished through the use of a chronosequence. This method has been routinely applied in other forest types (Crowell and Freedman 1994; Mund et al. 2002; Letcher and Chazdon 2009) as well as in *S. sempervirens* forests where they have been used to study specific impacts of logging (Loya and Jules 2007; Russell and Jones 2001; Russell 2009), but not over-all stand development. The objective of this study is to analyze natural regeneration of forest structure and composition in coast redwood forests, with the hypothesis that stand characteristics will tend toward old-growth conditions over time.

METHODS

Study Sites

Data was collected in the central range of the coast redwood forest, as defined by Sawyer et al. (2000) (Fig. 1). Study sites were located primarily in the Big River watershed, consisting of more than 2968 hectares of previously harvested coast redwood forest in Mendocino Co., California (California Department of Parks and Recreation 2006). Much of the watershed was managed as industrial timberland prior to its purchase by the Mendocino Land Trust in 2002, and subsequent transfer to the California State Parks as the Big River Unit of Mendocino Headlands State Park. The Big River watershed was an ideal location for this study due to the presence of second-growth redwood stands ranging from 15 to 127 yr old that had received no post-harvest manipulation.

The vegetation of the area is characteristic of the central range of the coast redwood forest with *Sequoia sempervirens*, *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*, and *Abies grandis*

(Douglas ex D. Don) Lindl. dominating the canopy, and *Lithocarpus densiflorus* (Hook. & Arn.) Rehder and *Tsuga heterophylla* (Raf.) Sarg. commonly occurring in the subcanopy. Under-story shrub species include *Polystichum munitum* (Kaulf.) C. Presl, *Vaccinium ovatum* Pursh, and *Rhododendron macrophyllum* D. Don. Common herbaceous understory species include *Oxalis oregana* Nutt., *Trillium ovatum* Pursh, *Viola sempervirens* Greene, *Calypso bulbosa* (L.) Oakes, *Iris douglasiana* Herb., *Tiarella trifoliata* L., and *Achlys triphylla* (Sm.) DC. The soils of the area are derived from the Franciscan assemblage, consisting mainly of sandstone and marine sediments. Typically, winters are cool and wet with an annual precipitation of 2500 mm or more (Sawyer et al. 2000). Summers are mild with moisture from intermittent fog providing up to 30% of the water requirements of *S. sempervirens* each year (Burgess and Dawson 2004).

For inclusion in this study, each site was required to have been previously clear-cut, be large enough for adequate sampling without edge effects (Russell and Jones 2001), and have not received post-harvest management such as seeding, thinning, or planting. Using these criteria, three study sites were selected in each of the five post-harvest age-classes (0–20, 21–40, 41–60, 81–100, and 101–130 yr) as well as the three unharvested old-growth reference sites. The post-harvest age-class 61–80 yr was not sampled due to a lack of sites in that age range that met the criteria of this study. Sites were selected using detailed timber harvest and land management history maps on a GIS platform (Rutland 2002). Old-growth reference sites included Montgomery Woods State Natural Reserve (462 ha) located in the Big River watershed; Russell Unit (49 ha) of Mendocino Headlands State Park located in the Brewery Creek watershed adjacent to the Big River Unit; and Hendy Woods State Park (342 ha) located in the Navarro River watershed to the south of the Big River. These three sites were selected because they represent the only sizable remaining old-growth stands in Mendocino County.

Data Collection

Twenty, 0.031 ha (20 m diam.) circular sample plots were randomly selected within each of the 18 study sites, and located using a handheld GPS receiver. Each sample plot was placed a minimum of 20 m from adjacent plots, 10 m from special habitats such as riparian areas and rock outcrops, and 200 m from adjacent age-class boundaries and main access roads. Plot size and sampling intensity were determined through a pilot study using the species-area curve method (Cain 1938) and are consistent with previous

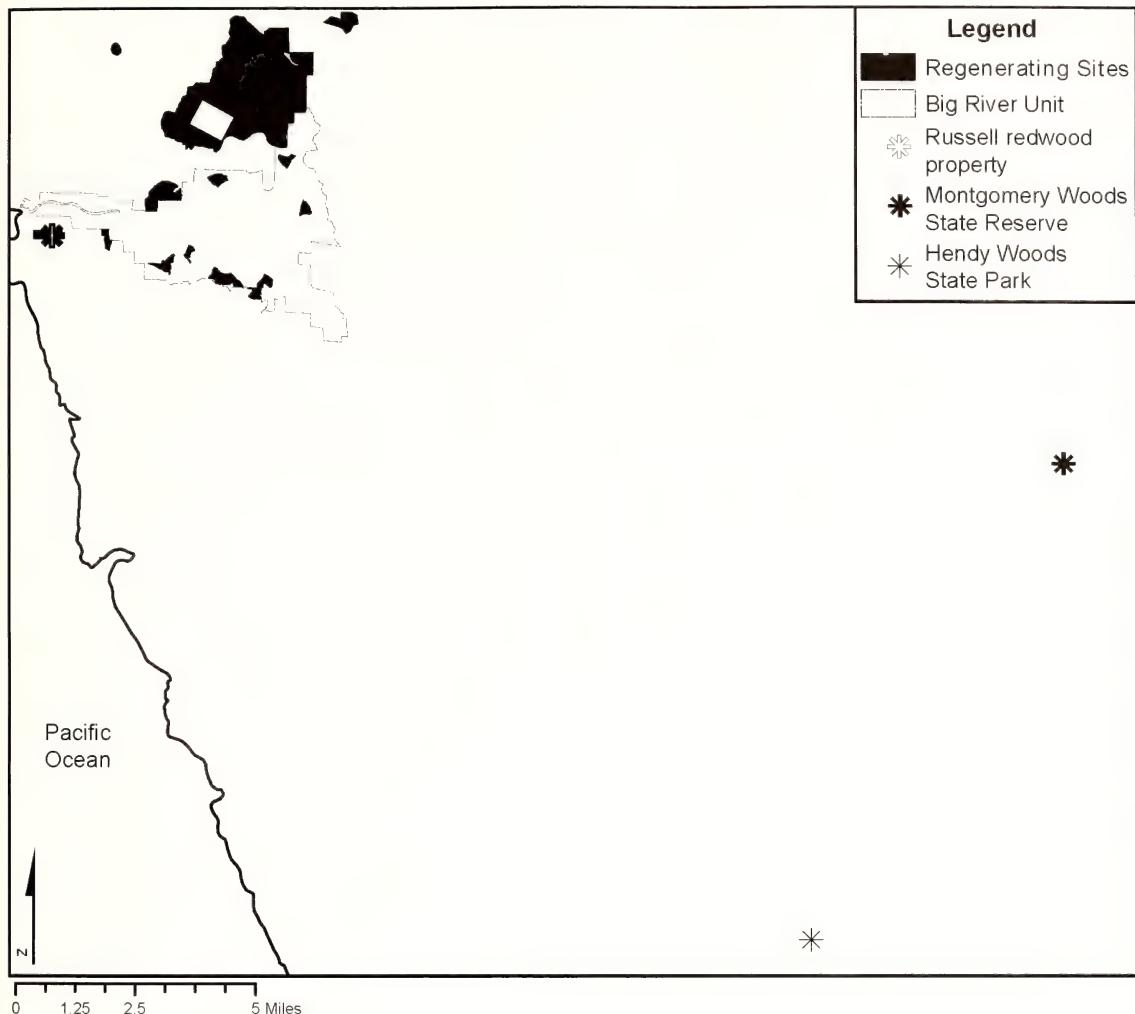


FIG. 1. Location of sampled regenerating stands and old-growth reference sites in Mendocino County, California.

research conducted in this forest type (Russell and Jones 2001; Loya and Jules 2007).

Data collected on each plot included: tree canopy cover (measured at plot center using a spherical crown densiometer with one reading taken in each of the four cardinal directions); the occurrence and abundance of each tree species; the diameter (measured at 1.4 m above ground level) of all individuals greater than one meter in height; and the occurrence and abundance of all tree seedlings. The percent cover for all understory species, including both herbs and shrubs, were determined using ocular estimates over the entire plot. In order to improve the accuracy of estimates plots were divided into eight sample wedges. Cover of each species was estimated in the field by two researchers and averaged. Species were identified using the Jepson manual of higher plants of California (Hickman 1993).

Data Analysis

As a preparatory procedure prior to conducting ANOVA, we constructed a correlation matrix to examine possible relationships between stand characteristics and stand age. Significant correlations were found for several variables including tree density, seedling density, basal area and dominance of tree species, canopy cover, shrub cover, herbaceous cover, species richness, Shannon-diversity (Weaver and Shannon 1949), and the cover of individual understory species including non-natives. One-way ANOVA analysis was used to test for differences among the means for each variable between age-classes and old-growth reference sites in a manner consistent with analysis of chronosequence data in other forest types (Pare and Bergeron 1995; Claus and George 2005; Delzon and Loustau 2005). Data

TABLE 1. STAND CHARACTERISTICS OF SIX AGE-CLASSES IN A CHRONOSEQUENCE OF POST-HARVEST DEVELOPMENT IN THE CENTRAL RANGE OF THE *SEQUOIA SEMPERVIRENS* FOREST. Age-classes sharing the same lower-case letter in each series were not significantly different, based on single factor ANOVA analysis ($\alpha = 0.05$).

Age class	Tree density (trees/ha)	Combined seedling density (seedlings/ha)	Redwood seedling density (seedlings/ha)	Basal area (m ² /ha)	Richness (species/plot)	Shannon- diversity
0-20 yr	2048 a	890 a	184 a	14.8 a	21.9 a	2.0 a
21-40 yr	1889 a	1152 b	291 a	22.9 b	18.4 b	2.0 a
41-60 yr	940 b	1243 b	311 a	55.3 c	18.6 b	2.2 b
81-100 yr	1260 c	1189 b	338 a	96.9 d	17.9 b	1.9 c
101-130 yr	906 b	829 a	516 b	102.5 e	18.0 b	1.9 c
Old-growth	763 b	917 a,b	643 b	362.2 f	16.9 b	1.8 c

were tested for homogeneity using the Bartlett's Chi-Square statistic, and post-hoc analyses were conducted using the Bonferroni test for pair-wise differences between groups. Principle components analysis (PCA) was used to characterize general trends in species cover between age-classes. PCA data was transformed with individual variable ranking to eliminate null values. Data analyses were conducted using Aable 2 statistical software (Gigawiz Ltd. Co., Tusla).

RESULTS

Tree Density, Dominance, and Diameter Distribution

The density of trees (>1 m in height) declined with stand age (Table 1). The highest density was measured in the two youngest age-classes with significantly lower densities found in all other age-classes. Initial statistical equivalence with old-growth reference sites was reached in the third age-class suggesting the occurrence of a natural thinning event up until 40 yr. Somewhat higher densities on the two oldest age-classes, compared to the old-growth, suggest that stand

thinning may continue at a reduced rate as the forest transitions toward old-growth conditions.

The combined density of tree seedlings exhibited little variation between age-classes. A somewhat higher number were found on sites ranging from 21-100 yr, however, all age-classes were statistically equivalent to old-growth. The density of *S. sempervirens* seedlings, however, exhibited a positive trend with stand age with the highest density found on the old-growth reference sites; statistical equivalence with old-growth was found for sites over 100 yr. No statistically significant relationship was found between stand age and the density of any other trees seedlings.

The average combined basal area per hectare increased with stand age exhibiting significantly higher values in each successive age-class (Table 1). Basal area did not reach statistical equivalence with old-growth stands within the timeframe of the chronosequence. Analysis of the relative dominance (specific basal area/total basal area) of the three most common tree species (*S. sempervirens*, *L. densiflorus*, and *P. menziesii*) indicated an increase in the relative dominance of *S. sempervirens* over time (Fig. 2), with *S. sempervirens* eclipsing all other species in the

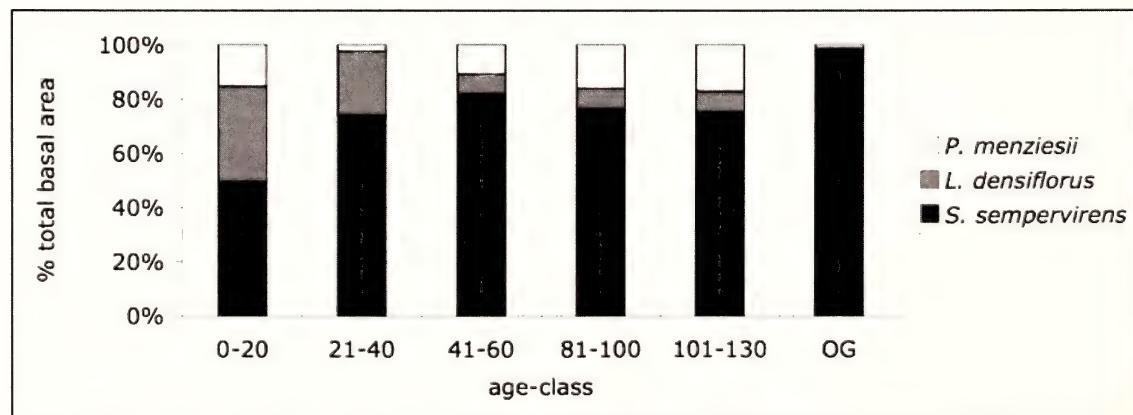


FIG. 2. Relative dominance (specific basal area/total basal area) of *Sequoia sempervirens*, *Lithocarpus densiflorus*, and *Pseudotsuga menziesii* across a 127-yr chronosequence of naturally regenerating *Sequoia sempervirens* stands.

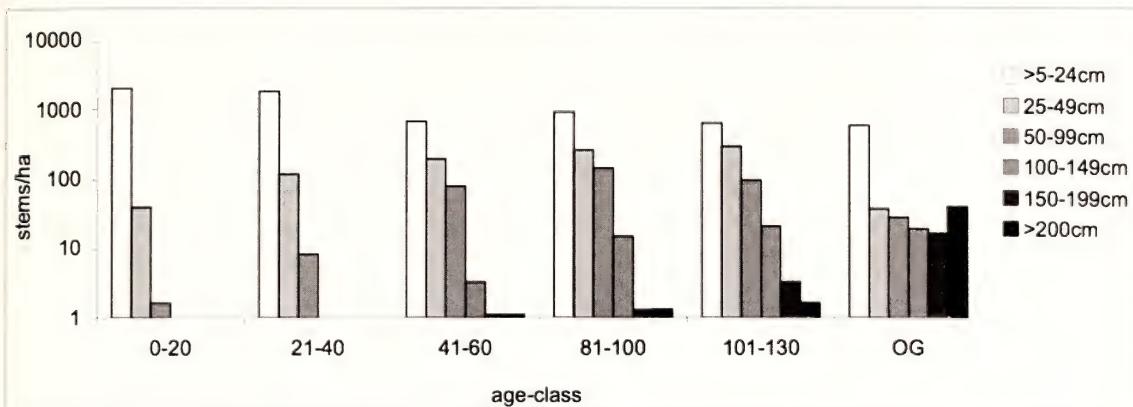


FIG. 3. Diameter distributions between six age-classes for all tree species combined on a post-harvest chronosequence in the central range of the *Sequoia sempervirens* forest.

old-growth age class. The highest relative dominance for *L. densiflorus* was found in the two youngest age-classes, with significantly lower values found for all subsequent age-classes. The relative dominance of *P. menziesii* varied throughout the chronosequence with its highest values found in the 81–100 yr and 100–130 yr age-classes.

An analysis of diameter distributions, based on size classes defined by Guisti (2007), indicated an increase in the density of larger diameter trees

over time (Fig. 3). The density of the smallest size-class of tree declined significantly in the early age classes, but showed no significant change after 40 yr. This result is consistent with a natural thinning event occurring early in the stand development process. Individual analysis of the diameter distributions of the three most common tree species (*S. sempervirens*, *L. densiflorus*, and *P. menziesii*) suggests a pulse of regeneration for each species early in the chronosequence (Fig. 4). It was also noted that *S. sempervirens* had the

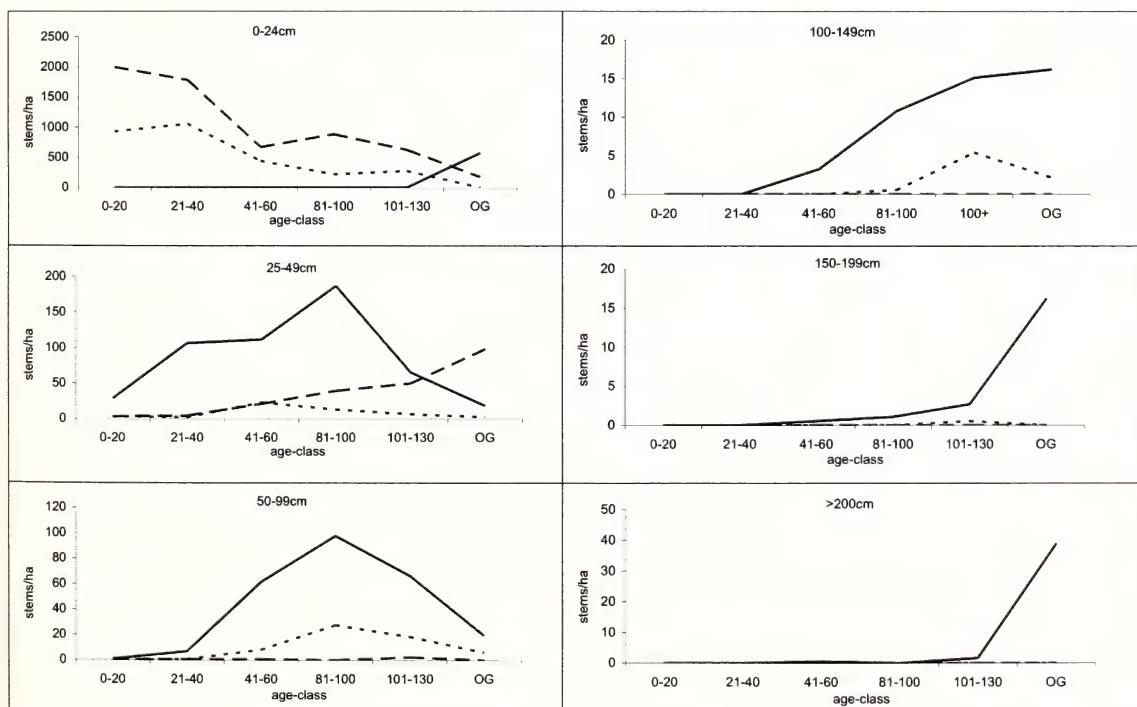


FIG. 4. Diameter distribution of three species on six age-classes combined on a post-harvest chronosequence in the central range of the coast redwood forest (solid line = *Sequoia sempervirens*; wide-dashed line = *Lithocarpus densiflorus*; narrow-dashed line = *Pseudotsuga menziesii*).

highest density of trees in all size-classes across the chronosequence with the exception of the smallest size-class (0–24 centimeter) where *L. densiflorus*, and *P. menziesii* dominated, and the 25–49 centimeter) size class where *P. menziesii* dominated in the old-growth.

Percent Cover of Canopy Layers

The percent cover of trees, shrubs, and herbs varied significantly between age-classes (Fig. 5). The lowest tree cover was recorded in the two youngest age-classes with cover statistically equivalent to old-growth found in stands older than 81 yr. Shrub cover was highest in the two youngest age-classes, significantly lower in the 41–60 yr age-class, and progressively higher thereafter, reaching statistical equivalence with old-growth in the two oldest age-classes. Herb cover was uniformly low, and statistically equivalent, in all second-growth sites compared to old-growth where it was more than three times greater.

Diversity and Species Distribution

One hundred twenty-seven plant species were recorded in the sample plots (Appendix 1). The highest species richness (species/plot) was found in the youngest age-class with lower, statistically equivalent, values in all other age-classes including old-growth (Table 1). The Shannon-diversity index (H') also exhibited a generally negative trend reaching statistical equivalence with old-growth in stands 81 yr and older. An H' peak was found for the 41–60 yr age class, possibly in response to the natural thinning event noted in the earlier age-classes.

Principal components analysis, using ranked percent cover of the 55 most common species, produced two axes that together explained 53.3% of the total variance with the first axis accounting for 35.9% and the second axis accounting for 17.4% (Fig. 6). The ordination illustrates grouping by age-class along the x-axis (PC 1) with positive eigenvalues associated with the oldest age-classes including *S. sempervirens* (0.33), *Trillium ovatum* (0.45), *Oxalis oregana* (0.36), *Viola sempervirens* (0.34), *Tiarella trifoliata* (0.32), and *Calypso bulbosa* (0.28); and negative eigenvalues associated with the younger age classes including *Lithocarpus densiflorus* (−0.31), *Lonicera hispida* Douglas (−0.34), *Whipplea modesta* Torr. (−0.32), and *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (−0.27). The y-axis (PC₂) was positively associated with *Vaccinium ovatum* (0.41) and *Rhododendron macrophyllum* (0.30); and negatively correlated with *Sequoia sempervirens* (−0.31) and *Oxalis oregana* (−0.31).

Ten non-native plant species were recorded within the chronosequence (Table 2). The cover of each of these species declined with stand age to the extent that no non-native species were recorded in stands older than 60 yr. The absence of non-natives in the older age-classes suggests a lack of successful long-term establishment. However, the year of introduction, and historic distribution of each species, must also be considered as a possible explanation for their absence in older stands. While species such as *Sonchus asper* (L.) Hill and *Stellaria media* (L.) Vill. have been present in the region since the middle of the 1800's, *Cortaderia selloana* (Schult.) Asch. & Graebn. and *Leontodon leysseri* (Vill.) M-rat may not have been present until the middle of the 1900's.

Additional analysis of understory species cover indicated that several species commonly associated with coast redwood forests increased with years since harvest. The cover of *C. bulbosa*, *T. ovatum*, and *V. sempervirens* increased to levels statistically equivalent to the old-growth reference sites within the timeframe of the chronosequence (Fig. 7a). The cover of *Iris douglasiana*, *Tiarella trifoliata* L., and *Achlys triphylla* also exhibited positive trends with stand age, but were significantly lower on all age-classes compared to old-growth (Fig. 7b).

DISCUSSION

In contrast to the "gap phase" succession process associated with old-growth coast redwood forests, the second-growth stands studied in our post-harvest chronosequence followed patterns similar to forest types that regularly experience stand scale disturbance. Results indicate a progression through the four phases of succession outlined by Oliver (1981), "stand re-initiation," "stem exclusion," "understory re-initiation," and "old-growth." Many stand characteristics including tree density, canopy cover, shrub-cover, species diversity, non-native species occurrence, and the cover of several redwood associated species reached old-growth equivalence. While total basal area, dominance of *S. sempervirens*, herb cover, and the cover of several other redwood associated species, all progressed toward, but did not reach, old-growth equivalence within the 127-yr timeframe of the chronosequence. In addition, the diameter distribution of trees within age-classes indicated a transition from stands characterized by a high density of small trees, to stands exhibiting a mixed size-class distribution. These results are consistent with the view that forests dominated by *S. sempervirens* have a high regenerative potential and are highly resilient following disturbance (Allen et al. 1996).

The assertion that natural processes of community development are sufficient management approaches for the regeneration of coast redwood

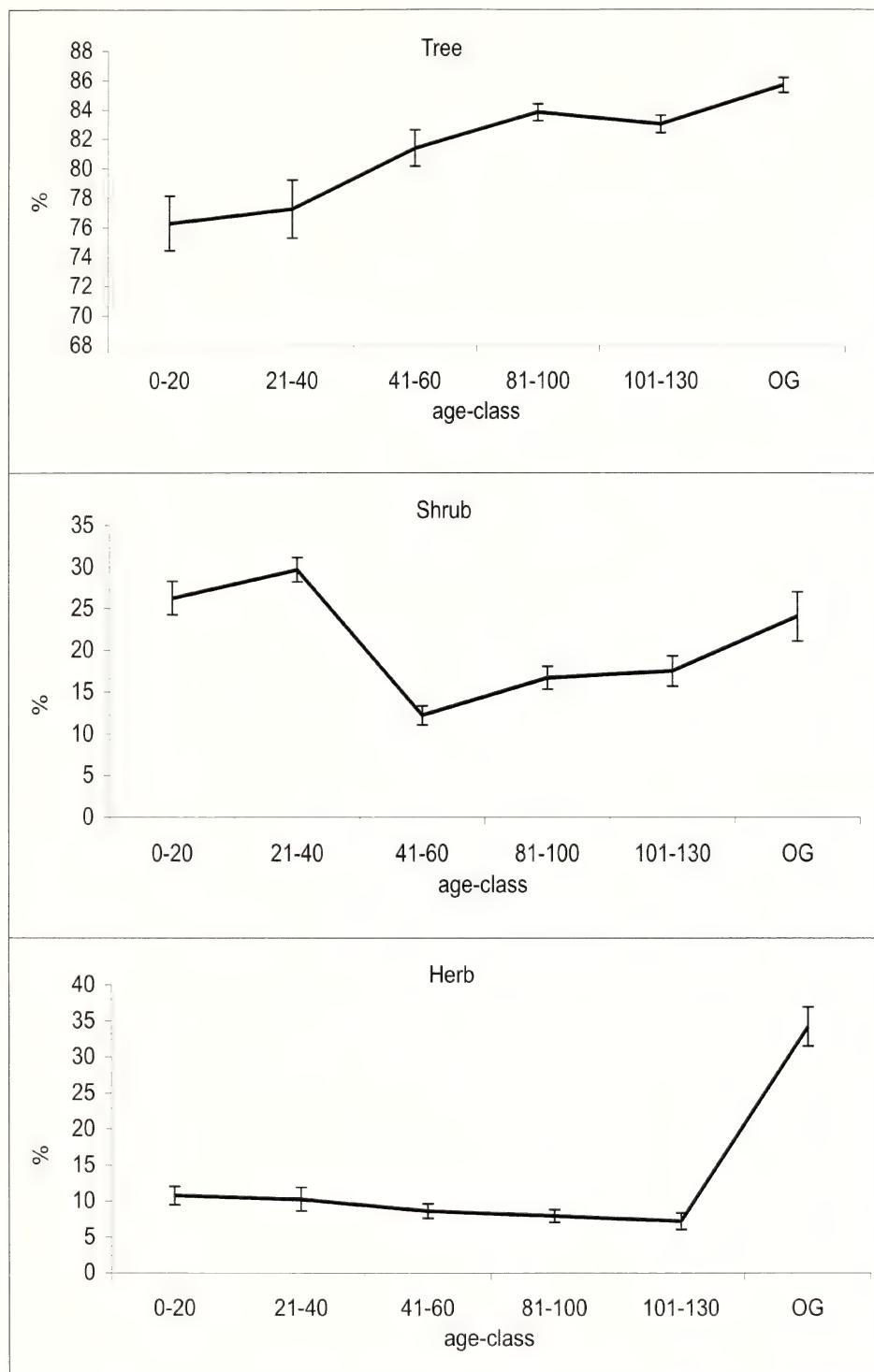


FIG. 5. Percent cover of trees, shrubs, and herbs on six age-classes on a post-harvest chronosequence in the central range of the *Sequoia sempervirens* forest; error bars indicate standard error.

forests (Busing and Fujimori 2002, 2005) is also supported by this research to some degree. The proliferation of *Trillium ovatum*, a species that is severely impacted by timber harvesting (Kahmen

and Jules 2005), as well as several other coast redwood associates within the timeframe of our chronosequence, is encouraging. However, not all coast redwood-associated species recovered com-

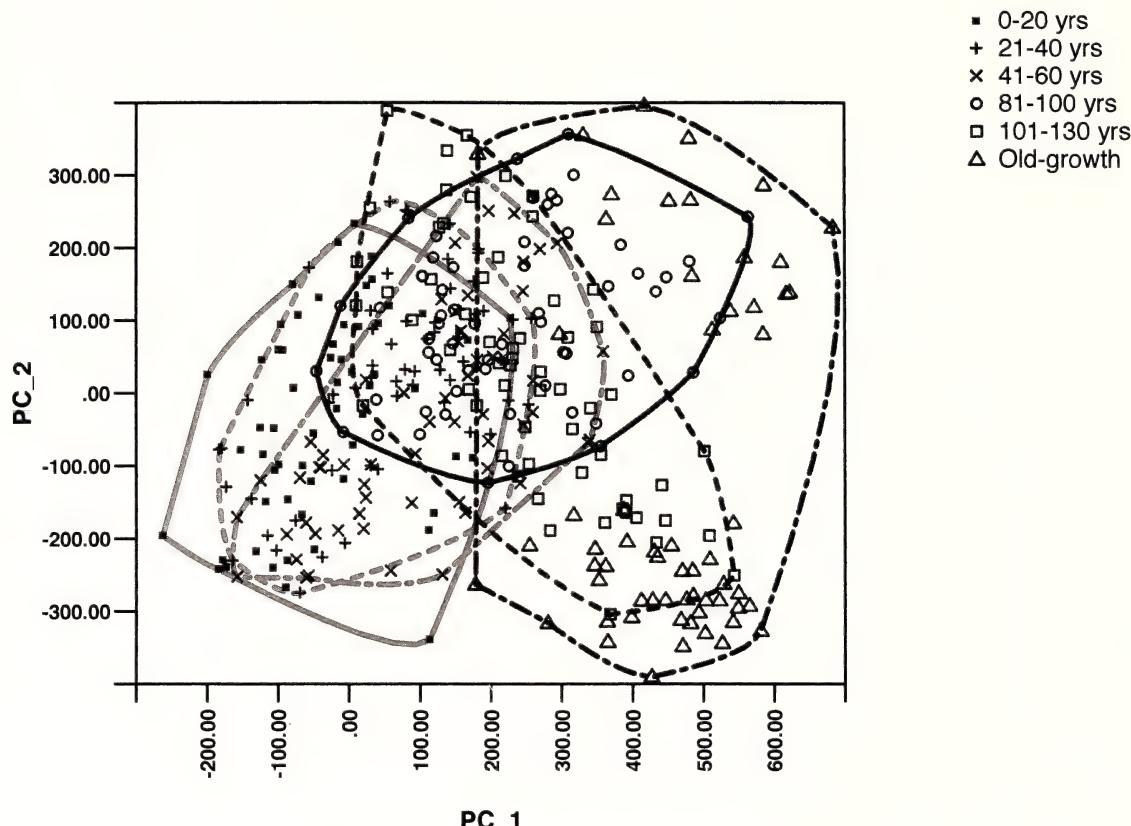


FIG. 6. Principle components for plant species across a 127-yr chronosequence of naturally regenerating *Sequoia sempervirens* stands. PC-1 explained 35.9% of variation. PC-2 explained an additional 17.4%. Convex outlines indicate post-harvest and old-growth age classes.

pletely, suggesting that reestablishment of the coast redwood understory is a lengthy process.

The ability to measure the full recovery of *S. sempervirens* stands following timber harvest was limited by the length of our chronosequence in relation to the life span of the dominant organism (>1500 yr). The study was also limited by gathering data exclusively at ground level.

Considering the volume and complexity of the old-growth coast redwood canopy, the full development of a stand may require several centuries (Sillett and Baily 2003). The study of post-harvest patterns of canopy development, as well as analysis of soil organism assemblages and wildlife habitat features, could increase insight into the long-term effects of timber harvest, and

TABLE 2. NON-NATIVE PLANT SPECIES RECORDED IN SIX AGE-CLASSES IN THE CENTRAL RANGE OF THE COAST REDWOOD FOREST. The estimated date of introduction is based on the earliest specimen records for each species in northern coastal California, retrieved from the Consortium of California Herbaria (http://ucjeps.berkeley.edu/cgi-bin/get_consor).

Species	Estimated date of introduction	Oldest age-class present
<i>Arabidopsis thaliana</i> (L.) Heynh. (Mouse Ear Cress)	1926	41–60
<i>Cirsium vulgare</i> (Savi) Ten. (Common Bull Thistle)	1900	41–60
<i>Cortaderia selloana</i> (Schult.) Asch. & Graebn. (Pampas Grass)	1941	41–60
<i>Hypochoeris glabra</i> L. (Smooth Cat's Ear)	1888	41–60
<i>Hypochoeris radicata</i> L. (Hairy Cat's Ear)	1900	41–60
<i>Lactuca saligna</i> L. (Willowleaf Lettuce)	1927	0–20
<i>Leontodon taraxacoides</i> (Vill.) Mérat (White-Flowered Hawk Bit)	1938	21–40
<i>Sonchus asper</i> (L.) Hill (Spiny Sow Thistle)	1861	21–40
<i>Stellaria media</i> (L.) Vill. (Common Chickweed)	1876	21–40
<i>Taraxacum officinale</i> F. H. Wigg. (Dandelion)	1895	0–20

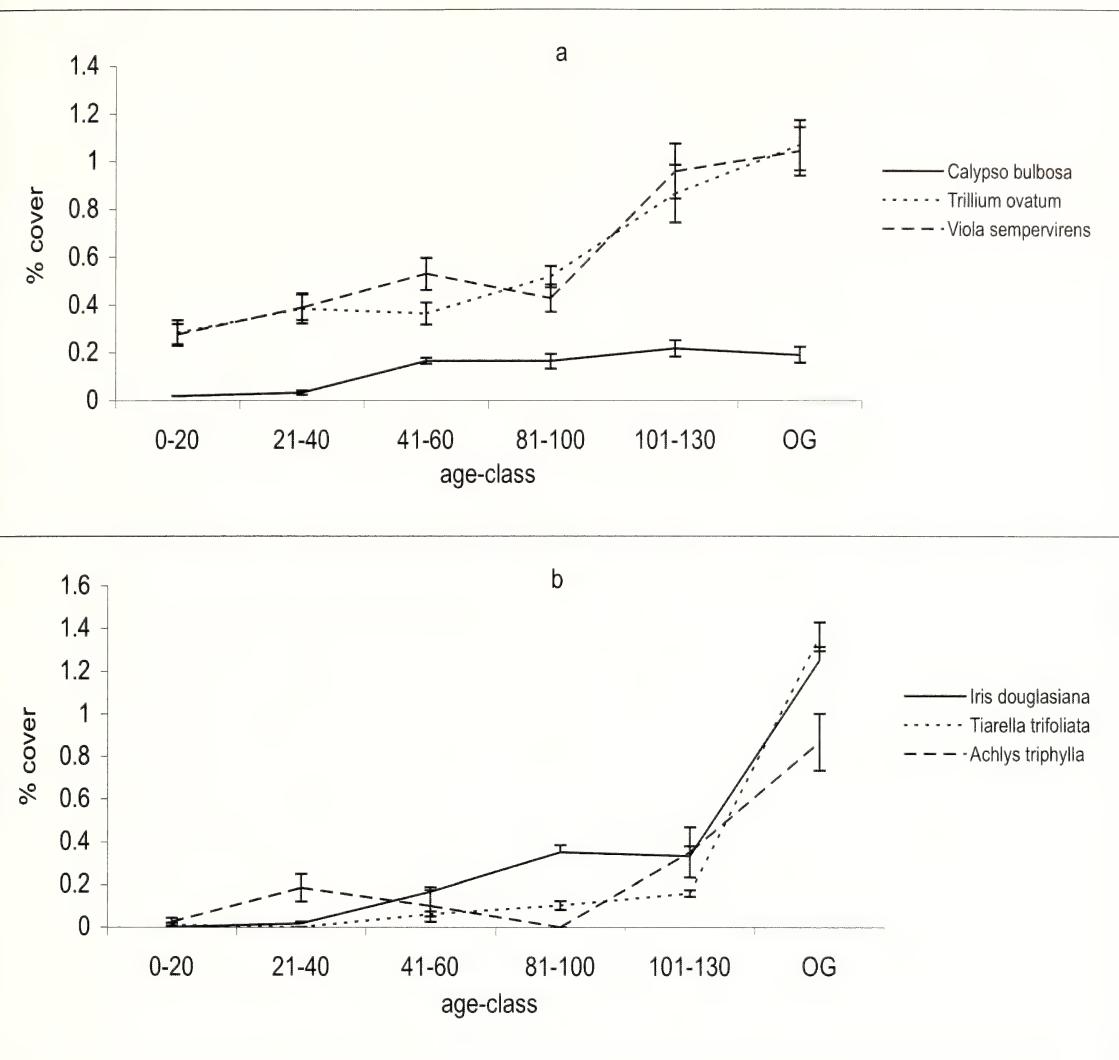


FIG. 7. Mean percent cover of coast redwood associated species on six post-harvest age-classes on a post-harvest chronosequence in the central range of the *Sequoia sempervirens* forest; error bars indicate standard error; a) represents species that reached OG equivalence, b) represents species that did not reach OG equivalence.

the regenerative potential of the entire forest community over time.

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APPENDIX 1

PLANT SPECIES RECORDED ACROSS SIX AGE-CLASSES ON A POST-HARVEST CHRONOSEQUENCE IN THE CENTRAL RANGE OF THE *SEQUOIA SEMPERVIRENS* FOREST

	Age class					
	0–20	21–40	41–60	81–100	101–130	OG
Trees (m²/plot)						
<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	0.01	0.00	0.04	0.26	<0.01	0.02
<i>Alnus rubra</i> Bong.	<0.01	0.01	0.01	<0.01	0.04	0.00
<i>Arbutus menziesii</i> Pursh	0.11	<0.01	0.00	0.05	<0.01	0.00
<i>Corylus cornuta</i> var. <i>californica</i> (A. DC.) Sharp	<0.01	0.00	0.00	0.00	0.00	<0.01
<i>Lithocarpus densiflorus</i> (Hook. & Arn.) Rehder	0.10	0.16	0.11	0.20	0.21	<0.01
<i>Myrica californica</i> Cham. & Schldl.	<0.01	<0.01	<0.01	<0.01	0.00	<0.01
<i>Pinus muricata</i> D. Don	0.00	0.00	<0.01	0.12	<0.01	0.01
<i>Pinus sabiniana</i> Douglas	0.00	0.00	0.00	0.00	<0.01	0.00
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>menziesii</i>	0.04	0.02	0.17	0.44	0.49	0.17
<i>Salix scouleriana</i> Hook.	<0.01	0.00	0.00	0.00	<0.01	0.00
<i>Sequoia sempervirens</i> (D. Don) Endl.	0.14	0.50	1.26	2.06	2.13	10.92
<i>Taxus brevifolia</i> Nutt.	<0.01	0.00	0.00	0.00	<0.01	0.00
<i>Torreya californica</i> Torr.	<0.01	<0.01	0.00	0.00	0.00	0.00
<i>Tsuga heterophylla</i> (Raf.) Sarg.	<0.01	<0.01	0.12	0.03	0.09	0.07
<i>Umbellularia californica</i> (Hook & Arn.) Nutt.	0.02	0.01	<0.01	<0.01	0.02	0.05
Shrubs (% cover/plot)						
<i>Arctostaphylos columbiana</i> Piper	1.08	1.30	0.00	0.00	0.00	0.00
<i>Baccharis pilularis</i> DC.	0.00	1.30	0.00	0.00	0.00	0.00
<i>Berberis aquifolium</i> Pursh	0.00	0.00	0.00	0.08	0.00	0.03

APPENDIX 1. CONTINUED.

	Age class					
	0-20	21-40	41-60	81-100	101-130	OG
<i>Berberis nervosa</i> Pursh	0.12	0.57	0.50	0.11	0.24	0.10
<i>Blechnum spicant</i> (L.) Sm.	0.00	0.15	0.10	0.43	0.10	1.18
<i>Ceanothus thyrsiflorus</i> Eschsch.	6.82	1.02	0.22	0.00	0.02	0.00
<i>Euonymus occidentalis</i> Torr.	0.00	0.00	0.00	0.00	0.00	0.09
<i>Gaultheria shallon</i> Pursh	0.18	0.54	0.15	2.48	1.62	7.17
<i>Lepechinia calycina</i> (Benth.) Epling	0.00	0.00	0.00	0.00	0.01	0.00
<i>Lonicera hispidula</i> Douglas	0.66	0.48	0.66	0.38	0.15	0.22
<i>Rhododendron macrophyllum</i> D. Don	1.24	1.24	0.38	2.46	1.78	4.28
<i>Ribes menziesii</i> Pursh	0.09	0.03	0.00	0.03	0.00	0.02
<i>Rosa gymnocarpo</i> Nutt.	0.05	0.08	0.13	0.03	0.05	0.20
<i>Rubus leucodermis</i> Torr. & A. Gray	0.12	0.23	0.22	0.00	0.00	0.35
<i>Rubus parviflorus</i> Nutt.	1.02	0.32	0.43	0.00	0.02	0.00
<i>Rubus spectabilis</i> Pursh	0.00	0.00	0.00	0.00	0.00	0.05
<i>Rubus ursinus</i> Cham. & Schldl.	0.24	0.14	1.00	0.14	0.01	0.04
<i>Symporicarpos albus</i> (L.) S. F. Blake	0.00	0.00	0.01	0.00	0.02	0.00
<i>Toxicodendron diversilobum</i> (Torr. & A. Gray) Greene	3.21	1.04	0.80	0.47	0.58	1.53
<i>Vaccinium ovatum</i> Pursh	6.82	5.35	1.87	5.67	4.71	1.35
<i>Vaccinium parvifolium</i> Sm.	0.38	0.27	0.30	0.74	0.39	2.85
Ferns (% cover/plot)						
<i>Adiantum aleuticum</i> (Rupr.) C.A. Paris	0.07	0.05	0.16	0.10	0.26	0.02
<i>Athyrium filix-femina</i> (L.) Roth	0.00	0.05	0.16	0.10	0.26	0.02
<i>Dryopteris arguta</i> (Kaulf.) Maxon	0.27	0.16	0.68	0.08	0.00	0.09
<i>Pentagramma triangularis</i> (Kaulf.) Yatsk., Windham & E. Wollenw.	0.58	0.18	0.10	0.02	0.02	0.02
<i>Polypodium californicum</i> Kaulf.	0.00	0.00	0.00	0.06	0.00	0.09
<i>Polystichum munitum</i> (Kaulf.) C. Presl	6.24	2.59	4.07	4.10	6.01	5.00
<i>Pteridium aquilinum</i> var. <i>pubescens</i> L. Underw.	0.93	1.14	0.55	1.06	0.39	1.62
<i>Woodwardia fimbriata</i> Sm.	0.00	0.00	0.00	0.03	0.00	3.08
Herbs (% cover/plot)						
<i>Achlys triphylla</i> (Sm.) DC.	0.03	0.18	0.10	0.00	0.35	0.87
<i>Actaea rubra</i> (Aiton) Willd.	0.02	0.01	0.09	0.02	0.15	0.11
<i>Adenocaulon bicolor</i> Hook.	0.05	0.00	0.08	0.08	0.07	0.80
<i>Agoseris retrorsa</i> (Benth.) Greene	0.01	0.05	0.00	0.00	0.00	0.00
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook.	0.03	0.38	0.00	0.00	0.00	0.00
<i>Anemone deltoidea</i> Hook.	0.00	0.00	0.00	0.00	0.00	0.02
<i>Aquilegia formosa</i> Fisch.	0.03	0.00	0.02	0.00	0.00	0.22
<i>Arabidopsis thaliana</i> (L.) Heynh.	0.04	0.04	0.03	0.00	0.00	0.00
<i>Aralia californica</i> S. Watson	0.00	0.00	0.00	0.05	0.00	0.08
<i>Asarum caudatum</i> Lindl.	0.12	0.27	0.05	0.03	0.63	0.36
<i>Calypso bulbosa</i> (L.) Oakes	0.02	0.03	0.17	0.16	0.22	0.09
<i>Calystegia occidentalis</i> (A. Gray) Brummitt	0.00	0.11	0.00	0.00	0.00	0.00
<i>Campanula prenanthoides</i> Durand	0.17	0.07	0.18	0.01	0.02	0.11
<i>Cardamine californica</i> var. <i>californica</i> (Torr. & A. Gray) Greene	0.06	0.07	0.18	0.76	0.25	0.27
<i>Chenopodium berlandieri</i> Moq.	0.02	0.00	0.00	0.00	0.00	0.00
<i>Chimaphila menziesii</i> (D. Don) Spreng.	0.00	0.00	0.01	0.10	0.05	0.01
<i>Chlorogalum pomeridianum</i> (DC.) Kunth	0.01	0.00	0.07	0.00	0.00	0.00
<i>Cirsium vulgare</i> (Savi) Ten.	0.13	0.06	0.18	0.00	0.00	0.00
<i>Claytonia perfoliata</i> Willd.	0.00	0.02	0.04	0.00	0.00	0.00
<i>Claytonia sibirica</i> L.	0.01	0.00	0.01	0.01	0.07	0.00
<i>Clintonia andrewsiana</i> Torr.	0.05	0.05	0.03	0.35	0.07	0.72
<i>Collomia heterophylla</i> Hook.	0.00	0.01	0.00	0.00	0.00	0.00
<i>Corallorrhiza maculata</i> Raf.	0.00	0.00	0.02	0.16	0.06	0.03
<i>Corallorrhiza striata</i> Lindl.	0.00	0.00	0.01	0.01	0.02	0.00
<i>Cordylanthus tenuis</i> A. Gray spp. <i>tenuis</i>	0.01	0.00	0.00	0.00	0.00	0.00
<i>Cortaderia selloana</i> (Schult.) Asch. & Graebn.	0.10	0.28	0.13	0.00	0.00	0.00
<i>Cynoglossum grande</i> Lehm.	0.02	0.02	0.03	0.10	0.00	0.00

APPENDIX 1. CONTINUED.

	Age class					
	0-20	21-40	41-60	81-100	101-130	OG
<i>Dicentra formosa</i> (Haw.) Walp.	0.17	0.13	0.01	0.00	0.18	0.00
<i>Disporum hookeri</i> (Torr.) G. Nicholson	0.37	0.25	0.49	0.39	0.35	1.53
<i>Epilobium angustifolium</i> L.	0.03	0.13	0.84	0.00	0.00	0.00
<i>Epilobium ciliatum</i> Raf.	0.01	0.00	0.03	0.00	0.00	0.00
<i>Equisetum arvense</i> L.	0.04	0.00	0.02	0.03	0.07	0.05
<i>Fragaria chiloensis</i> (L.) Duchesne	0.05	0.00	0.03	0.00	0.00	0.00
<i>Galium californicum</i> Hook. & Arn.	0.03	0.07	0.00	0.00	0.00	0.22
<i>Galium triflorum</i> Michx.	0.36	0.23	0.61	0.41	0.23	0.72
<i>Goodyera oblongifolia</i> Raf.	0.00	0.00	0.00	0.20	0.00	0.02
<i>Hemizonia corymbosa</i> (DC.) Torr. & A. Gray	0.00	0.00	0.04	0.00	0.00	0.00
<i>Holodiscus discolor</i> (Pursh) Maxim.	0.03	0.00	0.00	0.00	0.00	0.00
<i>Hypochaeris glabra</i> L.	0.03	0.03	0.01	0.00	0.00	0.00
<i>Hypochaeris radicata</i> L.	0.00	0.00	0.02	0.00	0.00	0.00
<i>Iris douglasiana</i> Herb.	0.00	0.02	0.02	0.04	0.03	0.13
<i>Lactuca saligna</i> L.	0.01	0.00	0.00	0.00	0.00	0.00
<i>Lathyrus vestitus</i> Nutt.	0.05	0.00	0.02	0.00	0.00	0.03
<i>Leontodon taraxacoides</i> (Vill.) Mérat	0.01	0.03	0.00	0.00	0.00	0.00
<i>Lithophragma glabrum</i> Nutt.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lotus purshianus</i> Clem. & E.G. Clem.	0.00	0.00	0.00	0.00	0.01	0.00
<i>Lotus stipularis</i> (Benth.) Greene	0.32	0.14	0.22	0.04	0.03	0.04
<i>Mimulus aurantiacus</i> Curtis	0.12	0.00	0.00	0.00	0.00	0.00
<i>Nemophila menziesii</i> Hook. & Arn.	0.01	0.00	0.00	0.00	0.00	0.00
<i>Nemophila parviflora</i> Benth.	0.05	0.00	0.02	0.00	0.00	0.00
<i>Oxalis oregana</i> Nutt.	1.68	0.97	0.77	1.63	3.00	23.27
<i>Petasites frigidus</i> (L.) Fries	0.02	0.00	0.00	0.00	0.00	0.00
<i>Polygonia californica</i> Nutt.	0.11	0.00	0.01	0.02	0.00	0.01
<i>Prunella vulgaris</i> L.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pyrola picta</i> Sm.	0.03	0.00	0.00	0.00	0.00	0.00
<i>Rhamnus alnifolia</i> L'Hér.	0.01	0.05	0.00	0.04	0.00	0.02
<i>Rhamnus purshiana</i> DC.	0.00	0.00	0.00	0.00	0.00	0.02
<i>Sanicula crassicaulis</i> DC.	0.02	0.00	0.02	0.00	0.00	0.00
<i>Satureja douglasii</i> (Benth.) Briq.	0.05	0.03	0.18	0.00	0.00	0.00
<i>Sceliopus bigelovii</i> Torr.	0.00	0.00	0.00	0.03	0.00	0.00
<i>Scrophularia californica</i> Cham. & Schldl.	0.02	0.20	0.00	0.00	0.00	0.00
<i>Senecio vugares</i> L.	0.00	0.02	0.00	0.00	0.00	0.00
<i>Smilacina racemosa</i> (L.) Link	0.11	0.00	0.04	0.05	0.04	0.17
<i>Smilacina stellata</i> (L.) Desf.	0.05	0.04	0.05	0.00	0.04	0.26
<i>Sonchus asper</i> (L.) Hill	0.03	0.04	0.00	0.00	0.00	0.00
<i>Stachys bullata</i> Benth.	0.27	0.23	0.24	0.00	0.02	0.03
<i>Stachys ajugoides</i> Benth.	0.00	0.00	0.00	0.08	0.00	0.58
<i>Stellaria crispa</i> Cham. & Schldl.	0.01	0.00	0.00	0.00	0.00	0.00
<i>Stellaria media</i> (L.) Vill.	0.00	0.01	0.00	0.00	0.00	0.00
<i>Stephanomeria exigua</i> Nutt.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Taraxacum officinale</i> F. H. Wigg.	0.02	0.00	0.00	0.00	0.00	0.00
<i>Tiarella trifoliata</i> L.	0.01	0.00	0.06	0.10	0.16	1.84
<i>Trientalis latifolia</i> Hook.	0.83	0.42	0.20	0.63	0.23	0.42
<i>Trillium chloropetalum</i> (Torr.) Howell	0.04	0.00	0.00	0.05	0.00	0.50
<i>Trillium ovatum</i> Pursh	0.28	0.38	0.36	0.86	0.52	1.07
<i>Urtica dioica</i> subsp. <i>holosericea</i> (Nutt.) Thorne	0.00	0.00	0.00	0.00	0.02	0.00
<i>Vancouveria planipetala</i> Calloni	0.46	0.29	0.21	0.33	0.18	0.01
<i>Veratrum californicum</i> Durand	0.00	0.00	0.00	0.03	0.00	0.22
<i>Vicia americana</i> Muhl. ex Willd.	0.01	0.00	0.00	0.00	0.00	0.00
<i>Viola glabella</i> Nutt.	0.00	0.00	0.00	0.02	0.08	0.93
<i>Viola sempervirens</i> Greene	0.28	0.40	0.53	0.96	0.44	1.03
<i>Whipplea modesta</i> Torr.	1.15	1.15	1.28	0.20	0.23	0.19
<i>Yabea microcarpa</i> (Hook. & Arn.) Koso-Pol.	0.03	0.03	0.00	0.00	0.00	0.00

REDISCOVERY OF *PLAGIOBOTHRYS HYSTRICULUS* (BORAGINACEAE) AND NOTES ON ITS HABITAT AND ASSOCIATES

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ABSTRACT

The rediscovery of bearded popcorn flower, the last confirmed collection of which was in 1892, is documented. The species is endemic to Napa, Solano, and Yolo counties, California, where it grows in vernal pools, vernal swales, and other moist areas in grasslands. Associated species include wetland and upland grasses and forbs typically found in the vernal pool-grassland ecotone.

Key Words: Boraginaceae, endemism, *Plagiobothrys hystriculus*, rare species, vernal pools.

Bearded popcorn flower, *Plagiobothrys hystriculus* (Piper) I. M. Johnst., is a rare plant previously confirmed from only two collections from Solano Co. The last known confirmed collection was made in 1892 by Willis Jepson, whose specimens became the type of *Allocarya hystricula* Piper (Piper 1920). Jepson's specimens cited the Montezuma Hills as the general collection location but provided no other detail. The other collection was made by Katherine Brandegee in 1883. Brandegee cited her collection locality as Elmira, north of the present Jepson Prairie, where she collected many grassland and vernal pool plants. The exact location of her collection site is unknown; all of the land in the vicinity of Elmira has long since been converted to agriculture. One other partial specimen apparently collected by K. Brandegee exists (UC101495), although no date or location information is associated with the specimen.

Because *Plagiobothrys hystriculus* was known only from two historic collections and no subsequent confirmed observations of it had been made, the California Native Plant Society (2001) had listed the species as extinct. Numerous attempts by botanists over many years (including the authors of this report) to relocate the species in the Montezuma Hills area apparently had been unsuccessful (T. Messick, ICF International, personal communication). Nevertheless, *P. hystriculus* was one of the 33 plant and animal species associated with vernal pools that were included in the “Recovery Plan for Vernal Pool Ecosystems of California and Southern Oregon” (United States Fish and Wildlife Service 2005). Although not listed as threatened or endangered, it was included in the Recovery Plan to put conservation actions in place should it be rediscovered.

REDISCOVERY

In May 2005, B. Schafer and M. Widdowson rediscovered and collected *Plagiobothrys hystriculus* in the Montezuma Hills during pre-project botanical surveys. The specimen was seen and identification confirmed by T. Messick, author of the *Plagiobothrys* treatment for the Jepson Manual (Messick 1993); the specimen was also compared with the isotype housed at the Jepson Herbarium, making this the first confirmed observation in almost 114 yr. Based on Schafer and Widdowson's description of the habitat in which the plants were found, R. Preston located two additional populations during surveys for an adjacent project. In 2006, after confirming that the species was present at the Montezuma Hills localities, Preston conducted a search for *Plagiobothrys hystriculus* at two vernal pool preserves (Wilcox Ranch, Jepson Prairie) located geographically intermediate between the Montezuma Hills and Elmira, successfully finding populations at both sites.

Although ours are the first confirmed collections of *Plagiobothrys hystriculus* since 1892, we are not the first to recollect the species. A subsequent search of the herbarium at the University of California, Davis (DAV) and the University of California/Jepson Herbaria (UC/JEPS) turned up additional specimens that had been misdetermined as *P. acanthocarpus* (Piper) I. M. Johnst., *P. greenei* (A. Gray) I. M. Johnst. or *P. glyptocarpus* (Piper) I. M. Johnst. The late Professors Beecher Crampton and John Tucker, both botanists at U. C. Davis, collected *P. hystriculus* specimens at or near Jepson Prairie in the 1960's and 1970's. Bob Holland, the noted vernal pool authority, also collected *P. hystriculus* at Jepson Prairie in 1976 and again in 1981. Jake Ruygt collected specimens in Napa Co. in 1998 while collecting for his Napa County flora project, and Ayzik Solomeshch collected *P. hystriculus* in 2002 while sampling vernal pools in Solano Co.

Why has this species been so difficult to locate? There are several likely explanations. Most of the land in the Montezuma Hills is privately owned

and not accessible for searches. The survey window for the species appears to be very narrow, as the blooming period lasts for only about three weeks, from the last week of April to the second week of May, and the plants are well into fruit and senescing by mid-May. The plants themselves are low and spreading, sometimes growing under a dense cover of *Lolium multiflorum* Lam., making detection extremely difficult. The plants are locally uncommon, occurring in small scattered stands, typically consisting of 10 to 20 plants. Annual variation in rainfall may also affect the ability of field workers to locate this species during any given year. The higher than average rainfall in 2005 and 2006 may have created optimal conditions for observing the species.

DISTRIBUTION

As currently known, the primary range of *Plagiobothrys hystriculus* consists of an approximately 150 square-mile area in central Solano Co., bordered to the south by the Montezuma Hills, to the north by Alamo and Ulatis creeks, and to the east by the Yolo Bypass. Another disjunct population occurs in Napa Co. The elevation range is from about 5 ft above sea level to about 870 ft above sea level. Although these observations have considerably expanded the known distribution of *P. hystriculus*, the species remains extremely rare and should remain a species of conservation concern. Fortunately, many of the new occurrences are located in vernal pool preserves.

HABITAT AND ASSOCIATES

Previous habitat characterizations described the habitat of *Plagiobothrys hystriculus* as "low plains" (Jepson 1925) or "grassy hillsides and plains" (Abrams 1951). Messick (1993) indicated that the habitat probably consisted of vernal pools or other wet sites, similar to other species in *Plagiobothrys* section *Allocarya*. Our observations indicate that *P. hystriculus* occurs in vernal pools and vernal swales and also in other vernally moist areas in grasslands that do not pond for significant duration but have saturated soil for long periods during the rainy season. Plants associated with *P. hystriculus* are those species commonly found at the ecotone between vernal pools and the adjacent annual grassland, including both native and introduced grasses and forbs (Table 1).

Most documented populations of *Plagiobothrys hystriculus* occur where soils have been mapped as San Ysidro sandy loam or Solano loam (Bates 1977). These soil series have increased clay content in the subsoil, which results in very slow permeability, and wetlands occur where swales or basins are present. One

population is on soil mapped as Rincon clay loam and another is on soil mapped as Capay clay (Bates 1977). The latter soil series have slow permeability but are less likely to support wetlands.

MORPHOLOGICAL COMPARISONS

The Jepson Manual key to the species of *Plagiobothrys* (Messick 1993) generally works well for section *Allocarya*. However, persons unfamiliar with the nutlet morphology or with the corresponding terminology could experience difficulty using the key. *Plagiobothrys hystriculus* is one of only four species (*P. acanthocarpus*, *P. austinae* [Greene] I. M. Johnst., *P. greenei*, *P. hystriculus*) that have prickles, large (ca. 1 mm) spine-like projections, on the abaxial nutlet surface (Fig. 1b–d). The prickles on these species are also beset with short, hair-like bristles that spread at right angles or curve towards the base of the prickles. Several other *Plagiobothrys* species have nutlets with bristles (*P. leptocladius* [Greene] I. M. Johnst., *P. hispidulus* [Greene] I. M. Johnst., *P. humistratus* I. M. Johnst., *P. scriptus* [Greene] I. M. Johnst.); however, all of these species lack prickles. *Plagiobothrys glyptocarpus* (Fig. 1a) and *P. trachycarpus* I. M. Johnst. (Fig. 1e) sometimes have very short prickles (ca. 0.1–0.2 mm) lacking bristles.

KEY TO THE *PLAGIOBOTHRYS* SPECIES WITH BOTH PRICKLES AND BRISTLES

1. Prickles on nutlet margins and abaxial ridge only; nutlet surface smooth, ridges or papillae obscure *P. austinae*
- 1' Prickles evenly distributed abaxially on nutlet; nutlet surface with ridges and/or papillae
 2. Nutlet surface prominently ridged abaxially and adaxially, the spaces between ridges with coarse papillae *P. acanthocarpus*
 - 2' Nutlet surface lacking ridges or with obscure adaxial ridges, finely papillate
 3. Nutlet surface papillae glabrous, ridges absent; bristles arched towards base of prickles; only lowermost flowers of inflorescence bracted *P. greenei*
 - 3' Nutlet surface papillate, papillae densely bristled, adaxial surface with obscure ridges; bristles short, straight; inflorescence bracted throughout *P. hystriculus*

SPECIMENS EXAMINED

The following collections summarize the known localities for *Plagiobothrys hystriculus* (additional collections/duplicates not listed have been distributed). USA. CALIFORNIA. Napa Co.: 4.7 mi N of first bridge on Berryessa-Knoxville Rd, J. Ruygt 3981 (JEPS). Solano Co.: Montezuma Hills, W. L. Jepson 21176 (JEPS),

TABLE 1. SPECIES OCCURRING WITH *PLAGIOTHYRS HYSTRICULUS*, RECORDED IN 24 1-M DIAMETER PLOTS IN SOLANO CO., CALIFORNIA.

Species	Frequency
<i>Lolium multiflorum</i> Lam.	95.83%
<i>Lythrum hyssopifolium</i> L.	83.33%
<i>Juncus bufonius</i> L.	62.50%
<i>Hordeum marinum</i> Hudson subsp. <i>gussoneanum</i> (Parl.) Thell.	50.00%
<i>Achyrrachaena mollis</i> Schauer	41.67%
<i>Eryngium aristulatum</i> Jepson	37.50%
<i>Crassula aquatica</i> (L.) Schönl.	29.17%
<i>Plagiobothrys stipitatus</i> (Greene) I. M. Johnst.	25.00%
<i>Geranium dissectum</i> L.	20.83%
<i>Bromus hordeaceus</i> L.	16.67%
<i>Cicendia quadrangularis</i> (Lam.) Griseb.	16.67%
<i>Plagiobothrys greenei</i> (A. Gray) I. M. Johnst.	16.67%
<i>Psilocarphus tenellus</i> Nutt.	16.67%
<i>Rumex crispus</i> L.	16.67%
<i>Briza minor</i> L.	12.50%
<i>Lasthenia fremontii</i> (A. Gray) Greene	12.50%
<i>Plagiobothrys bracteatus</i> (T. J. Howell) I. M. Johnst.	12.50%
<i>Plantago coronopus</i> L.	12.50%
<i>Pogogyne zizyphoroides</i> Benth.	12.50%
<i>Ranunculus muricatus</i> L.	12.50%
<i>Trifolium depauperatum</i> Desv.	12.50%
<i>Triphysaria eriantha</i> (Benth.) T. I. Chuang & Heckard	12.50%
<i>Cotula coronopifolia</i> L.	8.33%
<i>Deschampsia danthonioides</i> (Trin.) Munro	8.33%
<i>Downingia concolor</i> Greene	8.33%
<i>Erodium botrys</i> (Cav.) Bertol.	8.33%
<i>Limnanthes douglasii</i> R. Br.	8.33%
<i>Phalaris lemmonii</i> Vasey	8.33%
<i>Trifolium dubium</i> Sibth.	8.33%
<i>Veronica peregrina</i> L.	8.33%
<i>Aira caryophyllea</i> L.	4.17%
<i>Avena barbata</i> Link	4.17%
<i>Brodiaea elegans</i> Hoover	4.17%
<i>Convolvulus arvensis</i> L.	4.17%
<i>Holocarpha virgata</i> (A. Gray) Keck	4.17%
<i>Lasthenia californica</i> Lindl.	4.17%
<i>Lasthenia glaberrima</i> A DC.	4.17%
<i>Lotus corniculatus</i> L.	4.17%
<i>Plagiobothrys leptocladus</i> (Greene) I. M. Johnst.	4.17%
<i>Pleuropogon californicus</i> (Nees) Benth. ex Vasey	4.17%
<i>Poa annua</i> L.	4.17%
<i>Psilocarphus oregonus</i> Nutt.	4.17%
<i>Trifolium gracilentum</i> Torr. & A. Gray	4.17%
<i>Vulpia myuros</i> (L.) C. C. Gmel.	4.17%

isotype); Elmira, *K. Brandegee*, May 1883 (UC); 2 mi NE of Dozier Station, at jct Brown and Robbins roads, *B. Crampton* 6334 (AHUC); 2 mi SW of Dozier Station, *B. Crampton* 8700 (UC, AHUC); on N side of small road running W from intersection of Cook Lane and Sacramento Northern Railroad, ca. 1/2 mi W of this intersection, *J. M. Tucker* 4348 (DAV); N of Alkali Lake, Dozier, *R. Holland* 167 (UC); Jepson Prairie TNC Preserve, Section 23, *R. Holland* 1082 (UC); Gridley Ranch, 1 mi N from intersection of Hastings Rd and Salem Rd, *A. Solomeshch*, 27 Apr 2002 (DAV); Montezuma Hills, approximately 1 mi S of the junction of CA

Hwy 12 and CA Hwy 113, *Brad D. Schafer* 135 & *Margaret Widdowson* (JEPS), *Brad D. Schafer* 137 & *Margaret Widdowson* (DAV); Montezuma Hills, approximately 1.5 mi S of Hwy 12 and E of Olsen Rd, *R. E. Preston* 2347 (JEPS); Kirby Hill, at toe of north slope, *R. E. Preston* 2348 (DAV); 4.6 mi E of Travis Air Force Base, at Wilcox Ranch Preserve, *R. E. Preston* 2383 (DAV); 3 mi E of Travis Air Force Base, at Wilcox Ranch Preserve, *R. E. Preston* 2389 (DAV); Jepson Prairie Preserve, 1.4 mi SSW of the intersection of Cook Lane and Hwy 113, *R. E. Preston* 2393 (DAV). **Yolo Co.:** DFG Tule Ranch, *C. W. Witham* 1562 (DAV).

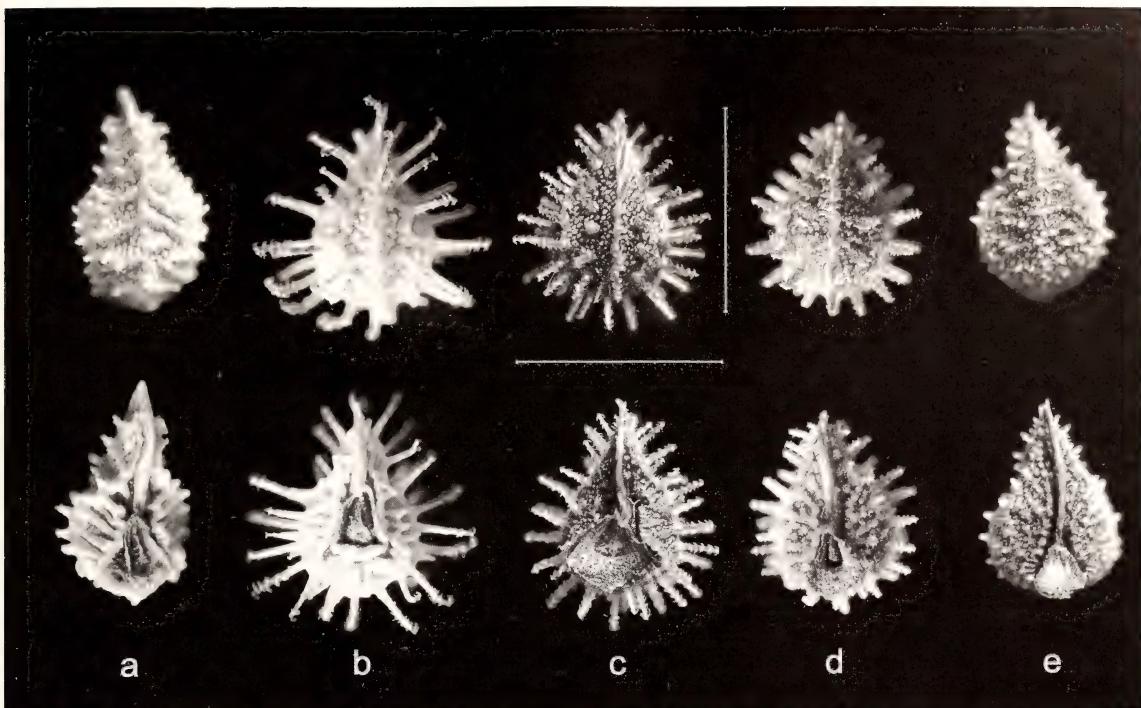


FIG. 1. Comparison of the nutlets of five *Plagiobothrys* species. a. *P. glyptocarpus*. b. *P. acanthocarpus*. c. *P. greenei*. d. *P. hystriculus*. e. *P. trachycarpus*. Scale bars = 3.0 mm.

ACKNOWLEDGMENTS

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TAXONOMIC NOVELTIES FROM WESTERN NORTH AMERICA IN *MENTZELIA* SECTION *BARTONIA* (LOASACEAE)

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ABSTRACT

Recent field collections and surveys of herbarium specimens have raised concerns about species circumscriptions and recovered several morphologically distinct populations in *Mentzelia* section *Bartonia* (Loasaceae). From the Colorado Plateau, we name ***M. paradoxensis*** from Paradox and Gypsum valleys of western Colorado, which is closely related to *M. marginata*. We name ***M. holmgreniorum*** from northeastern Arizona and ***M. filifolia*** from the northern border region of Arizona and New Mexico, both of which share morphological similarities with *M. lagarosa*, *M. laciniata*, and *M. conspicua*. From north central New Mexico, we name ***M. sivinskii***, which is most closely related to *M. procera* and *M. integra*. We describe three varieties of *M. longiloba*, including ***M. longiloba* var. *yavapaiensis***, which is distributed throughout Arizona, ***M. longiloba* var. *pinacatensis***, which is narrowly distributed in the Pinacate Desert of Sonora, Mexico, and the northern Chihuahuan Desert ***M. longiloba* var. *chihuahuaensis***. We propose the new combinations ***M. lagarosa*** and ***M. procera*** to alleviate the polyphyly of *M. pumila*.

Key Words: Cryptic species, intermountain West, new species, polyphyletic taxa, systematics.

Mentzelia section *Bartonia* (Loasaceae) is a monophyletic group (Hufford 2003; Hufford et al. 2003; Schenk 2009) dispersed throughout the arid North American West. The taxonomy of the section and collection limitations (Thompson and Prigge 1986) have long encumbered a clear understanding of the biological diversity of the group. Collections made in the last two decades have expanded our knowledge of diversity in the section and resulted in the description of 15 new species. Many of these recently described species are associated with restrictive substrates (e.g., gypsum-rich soils) and are narrowly distributed (Prigge 1986; Holmgren and Holmgren 2002; Schenk et al. 2010).

As part of a revisionary study of *Mentzelia* section *Bartonia*, we have made extensive new collections of the group, especially to examine the distribution and circumscriptions of poorly delimited taxa. This fieldwork and an accompanying survey of herbarium collections indicated that some populations possess morphological states that could not be readily accommodated in existing taxa in section *Bartonia*. The possibility that the existing taxonomy of the section does not capture the diversity that is present among natural populations has led us to sample distinctive populations as part of phylogeny reconstructions based on molecular data to examine their relationships to better known species (Schenk 2009). We have used insights from the fieldwork,

survey of herbarium specimens, and the phylogenetic placements of distinctive populations as a guide to their taxonomic treatment. Our results indicate that several populations are independent evolutionary lineages that do not readily fit existing species circumscriptions, and we describe these entities as new species. Several evolutionary lineages found to be associated with *M. longiloba* J. Darl. are morphologically and geographically distinctive (Schenk 2009), and we describe these as varieties of *M. longiloba*. In addition, our related molecular phylogenetic studies (Schenk 2009) also indicate that *M. pumila* Torr. & A. Gray as treated by Darlington (1934) and Thorne (1986) is polyphyletic. In order to alleviate the polyphyly of *M. pumila*, we make two new combinations.

MATERIALS AND METHODS

Field observations of nearly all species of *Mentzelia* section *Bartonia* and a study of our recent collections and specimens, including types, in herbaria were used to assess population and species variation. Morphological measurements were taken with digital calipers, using a dissecting microscope when necessary. Leaf characters were measured separately for leaves on the lower 1/3 and upper 1/3 of main stem or renewal axes. Leaf measurements were not taken from secondary or higher order (lateral, nonrenewal) branches because they often differed in size and shape from those on main stems. Leaf lengths were measured from the distal tip of the lamina to the junction of the leaf base with stem. Leaf widths were measured at the widest point of the lamina.

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The rachis width was measured as the distance across the sinuses at the shortest length between lobes (if present) and at the widest point of the lamina. Lobe width (when lobes were present), a measure across lobes, was measured at mid-length for a lobe positioned at the widest point of the leaf. The number of lobes per leaf included the total number of lobes on both margins of the leaf. Trichome densities and composition on leaves were characterized for both abaxial and adaxial surfaces of the lamina, excluding the central vein and margins. Prophylls either subtended all flowers or were adnate to the ovary. Prophyll measurements were made for the most distal bract that either subtended a flower or was adnate to a flower ovary. Calyx lobe lengths were measured from the base of a lobe to its distal tip, excluding the calyx tube and hypanthium. Petal lengths were measured from the base of a petal to its distal tip. Petal and median antesepalous (=outermost) stamen widths were measured at their widest points. We characterized petals as narrowly to broadly spatulate, oblanceolate, or elliptic based on assessment of overall shape. Elliptical (broadest near mid-length) and oblanceolate (broadest distal to mid-length) petals largely lacked a differentiated claw and limb in contrast to spatulate petals, which had distinct claw and limb regions. Styles were measured from the top of the ovary to the tip of the stigma lobes. Flower colors were based on field observations using the Royal Horticultural Society color chart and label data on herbarium specimens. Capsule lengths were measured from the ovary base to the insertion of calyx/hypanthium at the ovary apex on mature fruits. We denoted capsules as cup-shaped when they are less than twice as long as wide and cylindrical when more than twice as long as wide. We measured four (only for *M. holmgreniorum*, which is known from few collections) to 36 specimens for each new entity described below, as well as numerous specimens of previously described species.

Seed surface characters were assessed using scanning electron microscopy (SEM). Three seeds or more per sampled taxon were examined. Seeds were obtained from herbarium specimens or from field collections, mounted on metal stubs, and coated in gold prior to imaging. Seeds were examined at 20 kV using a Hitachi S-570 SEM, and micrographs were made of two seeds per accession at 700 \times or 600 \times .

Locality data for populations were gathered during fieldwork and from herbarium specimens. Latitude and longitude for new collections were made in the field using GPS. If herbarium specimens lacked field measured coordinates, we used the township, range, and section (TRS) data to infer latitude and longitude coordinates using Graphical Locator (Gustafson 1995). GEOLo-

cate v2.13 (www.museum.tulane.edu/geolocate/) and Google Earth (earth.google.com/) were used to estimate latitude/longitude coordinates if only limited locality information was available. Distribution data that could not be georeferenced accurately were not included in distribution maps. To image distributions of species, we imported population locality coordinates into ArcGIS v9.2 (ESRI, Redlands, CA).

NEW COMBINATIONS

***Mentzelia procera* (Wooton & Standl.) J. J. Schenk & L. Hufford, stat. et comb. nov. *Nuttallia procera* Wooton & Standl., Contributions from the U.S. National Herbarium, 16: 150, 1913; *Mentzelia pumila* Torr. & A. Gray var. *procera* (Wooton & Standl.) J. Darl., Annals of the Missouri Botanical Garden, 21: 169, 1934.—Type: USA, New Mexico, White Sands, 18 August, 1907, *Wooton & Standley* s.n. (holotype: US; isotype: NMC).**

***Mentzelia lagarosa* (K. H. Thorne) J. J. Schenk & L. Hufford, stat. et comb. nov. *Mentzelia pumila* Torr. & A. Gray var. *lagarosa* K. H. Thorne, Great Basin Naturalist, 46: 558, 1986.—Type: USA, Utah, Uintah Co., T11S, R24E, S11, near Watson, Evacuation Creek, 10 mi., 173 degrees from Bonanza, 1708 m, on gravel, 1 August 1980, *Goodrich & Atwood* 14664 (holotype: BRY; isotype: NY).**

Mentzelia pumila was treated broadly as a taxon widely distributed in the North American West in the monograph of Loasaceae by Urban and Gilg (1900) and the revision of *Mentzelia* by Darlington (1934). In contrast, Hill (1977) argued that *M. pumila* was restricted to the Red Desert of Wyoming, and Holmgren et al. (2005) treated it as restricted to Wyoming and adjacent portions of southern Montana and northeastern Utah, recognizing the name as misapplied to populations outside of this area. Schenk (2009) recognized the range of *M. pumila* as identical to that inferred by Holmgren et al. (2005) and demonstrated that an exemplar for *M. pumila* from Wyoming is phylogenetically isolated from lineages referable to *M. pumila* var. *procera* (*sensu* Darlington 1934) from New Mexico and surrounding areas and *M. pumila* var. *lagarosa* (*sensu* Thorne 1986) from southern Utah and Nevada. The new combinations recognize *M. pumila*, *M. lagarosa*, and *M. procera* as independent evolutionary lineages.

The variety *lagarosa* was placed as part of *M. pumila* based on identical chromosome numbers ($n = 11$) and similar growth habit (Thorne 1986). The pinnatisect laminas and sinuate anticlinal cell walls of seed testal cells of *M. lagarosa* distinguish it from *M. pumila*, which has pinnately-lobed laminas and straight anticlinal walls on seed testal

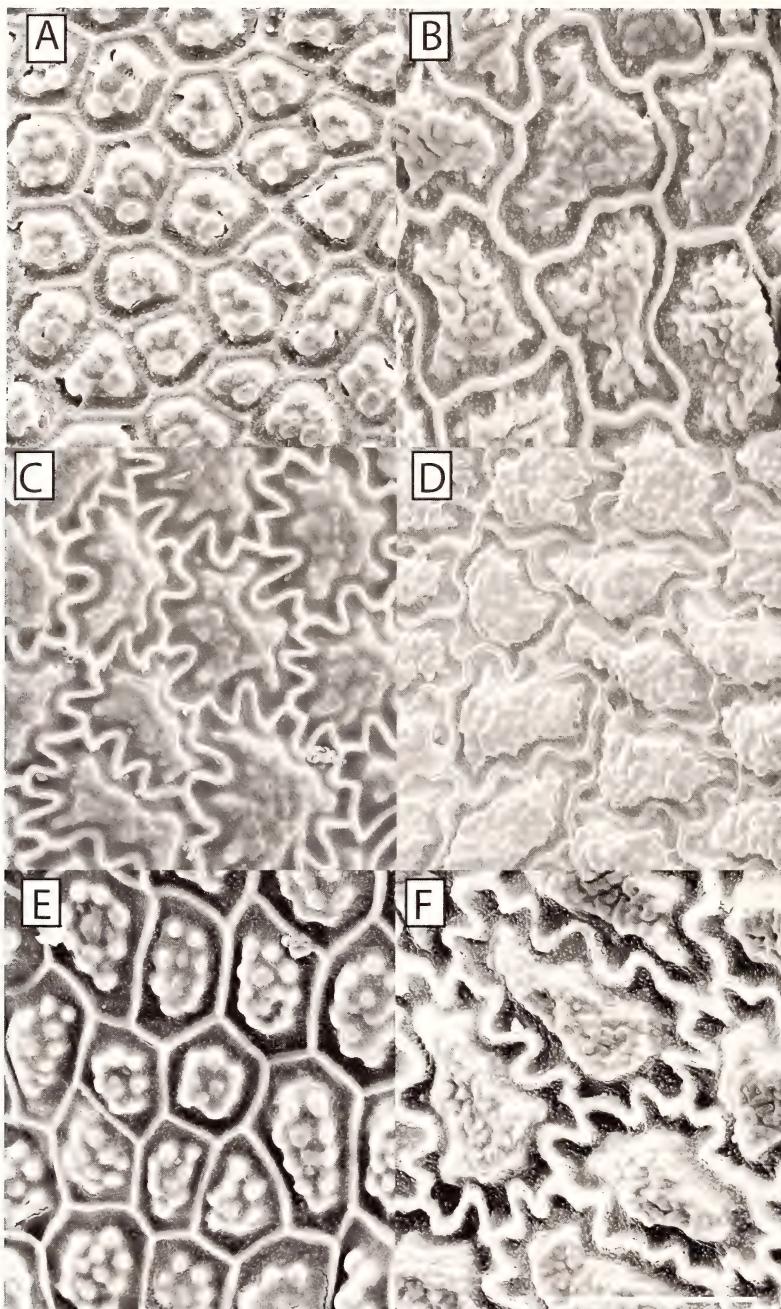


FIG. 1. Scanning electron micrographs of seed coat testal cells. A. *Mentzelia pumila*, B. *M. lagarosa*, C. *M. procera*, D. *M. filifolia*, E. *M. mexicana*, F. *M. multiflora*.

cells (Fig. 1). Populations of *M. lagarosa* occur in Colorado, Nevada, and Utah and are disjunct from the populations of *M. pumila*. The sister relationship of *M. lagarosa* remains uncertain (Schenk 2009); however, its narrowly dissected laminas, floral forms, and seed microsculpture characters are similar to taxa such as *M. laciniata* (Rydb.) J. Darl., *M. conspicua* T.A. Todsen, and *M. filifolia*, which is described below.

Mentzelia procera can be distinguished from *M. pumila* by sinuate versus straight anticlinal walls of seed coat testal cells (Fig. 1), respectively. The two species have overlapping morphological states, although petal lengths (9.5–16.3 mm vs. 11.5–20 mm) and capsule size (9.8–18.8 mm vs. 11.5–20 mm) are generally smaller in *M. procera* than in *M. pumila*. *Mentzelia procera* occurs in New Mexico and Colorado and is disjunct from *M.*

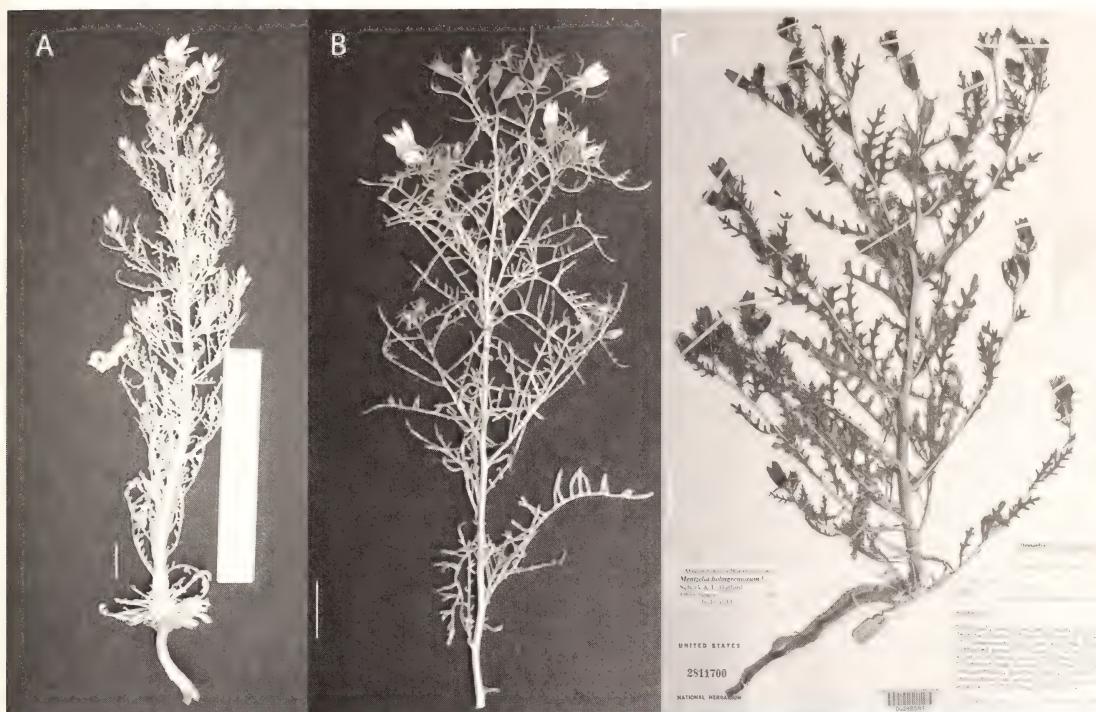


FIG. 2. Type specimens of newly described species. A. *M. paradoxensis*, B. *M. filifolia*, and C. *M. holmgreniorum*. Scale bars = 3 cm.

pumila. Molecular phylogenetic results (Schenk 2009) indicate that *M. procera* is more closely related to *M. integra* (M. E. Jones) Tidestr. and *M. sivinskii* (described below) than it is to *M. pumila*.

NEW SPECIES

***Mentzelia paradoxensis* J. J. Schenk & L. Hufford, sp. nov.** (Fig. 2A).—Type: USA, Colorado, Montrose Co., Paradox Valley, along Hwy 90, 12.7 rd mi SW of its jct with Hwy 141, E of Bedrock and Dolores River, 38°16.556'N, 108°47.632'W, 2 Jun 2006, L. Hufford 4475 (holotype: WS; isotype: COLO, NY, RM, UC, US).

Habitus singularis erectus, axillaris ramus brevis; caudex singularis; folia alterna elliptica vel lanceolata, margine lobata; petala 5, flavidus, spatulata; staminodia extima petaloidea; seminum testa in alam expansa.

Biennial herbs, up to 9 dm tall; taprooted. Main stem erect, straight, lateral branches on distal half of main stem or along the entire main shoot, lateral branches perpendicular to main stem along its basal region but branching acutely upward relative to the main stem along its distal region, branches straight; decumbent branches absent; epidermis pubescent, becoming white, exfoliating with age. Leaves alternate; rosette leaves narrowly to broadly spatulate, petiolate;

cauline leaves 38–91 × 6–17(21) mm, rachis width 1.6–4.7 mm; leaves on lower third of main stem oblanceolate, lanceolate, or elliptic, margins dentate to serrate or pinnate with 8–22 lobes, 4.5–11(15) mm apart, lobes nearly opposite, lobe slightly angled towards leaf apex or perpendicular to leaf axis, regular, up to 2–6.8(9) mm long with acute to occasionally rounded apices, margin revolute; leaves on upper third of main stem elliptic to lanceolate with non-clasping bases, margins dentate to serrate or pinnate with 8–16 lobes, 5.4–11.7(14) mm apart, lobes nearly opposite and slightly angled towards leaf apex or perpendicular to leaf axis, regular, up to 2.4–5(8.5) mm long with acute to occasionally rounded apices, revolute, pubescent, with greater density of simple grappling-hook, complex grappling-hook, and needle-like trichomes on abaxial surface, needle-like and occasionally simple grappling-hook trichomes on adaxial side. Inflorescence cymose, bract subtending inferior ovary entire, 2.5–11 × 0.4–1.1 mm. Calyx apices acute to attenuate, margin entire, 2.2–7.6 × 0.8–2.4 mm. Petals five, yellow, pubescent on abaxial surface, narrowly spatulate, 8.3–15(17.2) × 1.7–5.3 mm, apex acute to rounded. Androecium yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis papillate or not, anther occasionally twisted or remaining straight following dehiscence; outer whorls of stamens all fertile or fertile and

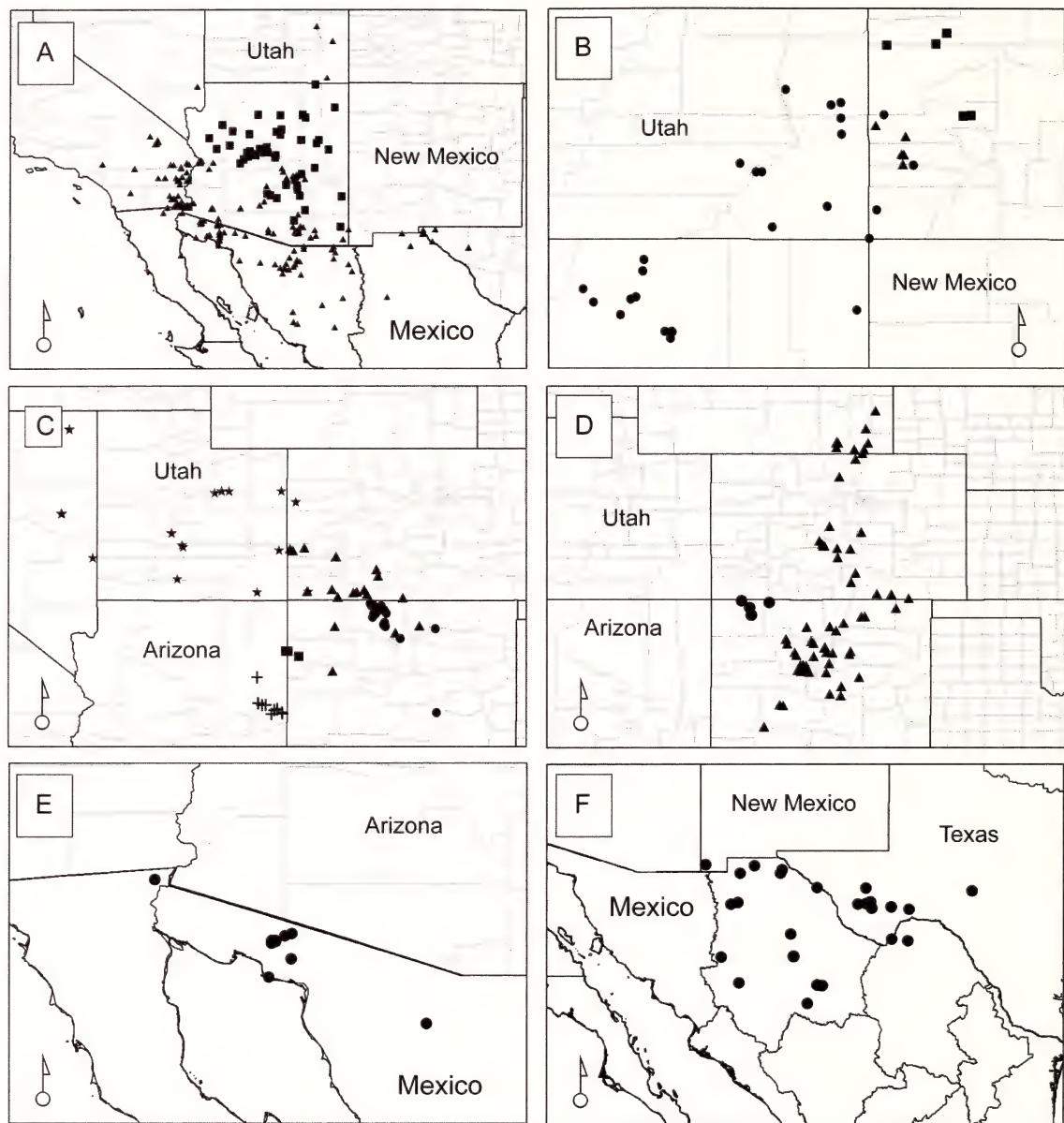


FIG. 3. Distributions of newly described taxa and selected relatives in USA and Mexico. A. *M. longiloba* var. *yavapaiensis* (■) and *M. longiloba* var. *longiloba* (▲). B. Distribution of *M. cronicostii* (●), *M. marginata* (■), and *M. paradoxensis* (▲). C. *M. laciniata* (▲), *M. conspicua* (●), *M. holmgreniorum* (+), *M. lagarosa* (★), and *M. filifolia* (■). D. Distribution of *M. sivinskii* (●) and *M. multiflora* (▲). E. *M. longiloba* var. *pinacatensis* (●). F. *M. longiloba* var. *chihuahuensis* (●).

staminodial, five outermost stamens in median antesepalous positions petaloid, narrowly spatulate, $6-13 \times 1.2-3.8$ mm, with or without anther, filament or staminode apex rounded to occasionally acute; second whorl of stamens all fertile. Ovary inferior, 3-carpellate with 3 placentae, funneliform; style 5.4–10.4 mm long, stigmas three. Fruit a capsule, cup-shaped, $5-9 \times 3.7-6.5$ mm, opening apically by three valves, base rounded, no prominent longitudinal costal ridges. Seeds pale grey to light brown with a white to light brown

wing, lenticular-ovoid, 1.7–2.7 mm long; testa reticulate, seed coat anticlinal cell walls straight to slightly wavy, central papillae generally 6–11 per cell. Chromosome number not determined.

Phenology: Flowering occurs from June to September.

Distribution: Populations occur in the Paradox and Gypsum Valleys of western Colorado at 1585–1964 m elevation (Fig. 3). Plants occur on road cuts, valley slopes and bottoms, and sparsely vegetated gypsum knolls.

Etymology: *Mentzelia paradoxensis* is named for the Paradox Valley of western Colorado.

Representative specimens: USA. COLORADO. **Montrose Co.:** W Paradox, *Payson* 2323 (RM); Paradox, *Walker* 157 (RM); Paradox Valley, along Hwy 90, 12.5 mi from its jct with Hwy 141, *Hufford* 4335 (WS); Paradox Valley, along Hwy 90, just E of Bedrock and 0.2 mi E of Dolores River and 1.2 mi W of its jct with River Rd (Rd Y11), *Hufford* 4336 (WS). **San Miguel Co.:** Hwy 141, on gypsum knoll across from mi post 36, on the western-most gypsum knolls of the E edge of the Big Gypsum Valley, W of Slick Rock, *Schenk* 972 (WS); Paradox Formation N of mi post 26 on Hwy 141, T46N R16W S14, *Atwood* 28894 (RM); 19 mi S of 141/145 jct on Hwy 141 between mi post 36–37, Big Gypsum Valley, T43N R16W S03, *Atwood* 28897 (RM); ca. 20 mi S of 141/145 jct on Hwy 141, Big Gypsum Valley, 38°01.480'N, 108°38.885'W, *Atwood* 28899 (RM); T44N R16W S31, *M. Ownbey* 1497 (GH, WS); Gypsum Valley, State Hwy 141, 11.6 km (7.2 mi) SW of Basin, T44N R16W S32, 38°01'32"N, 108°39'01"W, *N. & P. Holmgren* 13694 (WS).

The phylogenetic analysis of Schenk (2009) placed *M. paradoxensis* as sister to *M. marginata* (Osterh.) H. J. Thomp. & Prigge. The distribution of *M. paradoxensis* is south of the range of *M. marginata* (Fig. 3). Similar to *M. croniquistii* H. J. Thomp. & Prigge and *M. marginata*, *M. paradoxensis* has trichomes on the abaxial surfaces of petals. Collections of *M. paradoxensis* have been identified as *M. croniquistii*, and this may be a consequence not only of the petal trichomes but also their similar leaf laminas that are narrow and have long, acute lobes. *Mentzelia paradoxensis* differs from *M. croniquistii*, *M. marginata*, and other members of section *Bartonia* in having a shoot system characterized by many short lateral branches, at least in the lower portion of the main stem, that are nearly the same length along the main shoot. The numerous, short branches of *M. paradoxensis* give the whole shoot a cylindrical form and densely branched appearance. In contrast, both *M. croniquistii* and *M. marginata* have more candelabrum-shaped shoot systems. *Mentzelia paradoxensis* further differs from *M. croniquistii* in having smaller capsules. In contrast to *M. marginata*, which has leaf lobe apices that are rounded to occasionally acute, outermost stamens that are fertile, and long capsules (7–14.5 mm), *M. paradoxensis* is characterized by leaf lobes that have acute apices, outermost stamens that are staminodial or fertile, and short capsules (5–9 mm).

***Mentzelia filifolia* J. J. Schenk & L. Hufford, sp. nov.** (Fig. 2B).—Type: USA, New Mexico, McKinley Co., W of Gallup, Pima Rd, 2nd rd E of Hilltop Rd, 0.4 miles N of NM Route 264, 1.3 mi E of AZ border, 35°39.126'N, 109°01.571'W, 4 Aug 2006, *J. Schenk* 1659

(holotype: WS; isotypes: ARIZ, ASC, NMC, NY, RENO, UNM, US, UTC, WS).

Habitus singularis erectus; caudex singularis; folia alterna elliptica vel lanceolata, margine pinnatisecta filia; petala 5, flavidus, spatulata; staminodia extima petaloidea; seminum testa in alam expansa.

Biennial herbs, up to 7.5 dm tall; taprooted. Main stem erect, straight, lateral branches on distal half of main stems at acute angles, straight; epidermis pubescent, becoming white, shedding with age. Leaves alternate, rosette leaves unknown; caudine leaves 43–94(115) × 7.5–27(36) mm, rachis filiform, 1–2.4 mm wide; lower third of main stem oblanceolate to elliptic, margins filiform, pinnatisect with 8–20 lobes, 6–9 mm apart, nearly opposite, perpendicular, regular, up to 3.2–12(15.7) mm long with acute apex, margins revolute; upper leaves oblanceolate to elliptic with non-clasping bases, margins filiform, pinnatisect with 8–20 lobes, 7–12 mm apart, nearly opposite, perpendicular, regular, up to 5.6–17 mm long with acute apex, margins revolute; pubescent, abaxial surface with greater density of simple grappling-hook, complex grappling-hook, and occasionally with needle-like trichomes than adaxial surface, adaxial surface with needle-like trichomes. Inflorescence cymose, bract subtending inferior ovary entire to pinnate, 7–20 × 0.5–5.6 mm. Calyx 6–11 × 1–3 mm, apices acute to attenuate, margins entire. Petals five, yellow, glabrous on abaxial surface, oblanceolate, 14–18.5 × 3.6–6 mm, apex acute. Androecium yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis not papillate, straight following dehiscence; outer whorl of stamens fertile and staminodial, five outermost stamens in median antepetalous positions petaloid, oblanceolate, 10.3–14(18) × (1.4)2.5–4.4 mm, without anther, staminode apex acute; second whorl of stamens all fertile. Gynoecium 3-carpellate, ovary inferior, funnelform, 3 placentae; style 10–12.5(14) mm long, stigmas 3. Fruit a capsule, cylindrical, 11–19.3 × 5–7.5 mm, opening apically by three valves, base tapering, costal ridges running lengthwise diminutive. Seeds grey to light brown, lenticular-ovoid, winged, 2.9–3.2 mm; testa reticulate, seed coat anticlinal cell walls sinuate, central papillae generally 42–48 per cell. Chromosome number $n = 10$ (*Thompson* 3553 [US]).

Phenology: Plants flower from July to August.

Distribution: Populations occur in Apache Co., Arizona, and McKinley Co., New Mexico, where they occur on road-cuts and slopes of dark loam and rocky soils at 2122–2133 m elevation (Fig. 3).

Etymology: The specific epithet refers to the filiform lobes and narrow rachis of leaf laminas that serve to distinguish *M. filifolia* from other *Mentzelia* species of Arizona and New Mexico.

Representative specimens: USA. ARIZONA. **Apache Co.**: S of Wheatfields Lake, near turnoff to Crystal, along rd from Lukachukai to Fort Defiance, *Mason 2051* (ARIZ); Rte 12, 0.3 mi N of Rte 264, 35°39.792'N, 109°05.440'W, *Schenk 1660, 1661* (WS). NEW MEXICO. **McKinley Co.**: along rd to Lukachukai, about 3 mi N of Red Lake and 2 mi S of jct of rd to Crystal, *H. Thompson 3553* (ARIZ); Gallup, *Herrick 893* (US); July 1961 spoils, *W. Wagner 161* (UNM); May 1963 spoils, *W. Wagner 198* (UNM); near mine entrance along roadside, *W. Wagner 314* (UNM); on the S end of the July 1961 spoils, *W. Wagner 370* (UNM); N of Gallup, *Wooton 2800* (US), 3 Aug 1904, *Wooton s.n.* (US).

Darlington (1934) treated the populations recognized here as *M. filifolia* as part of *M. laciniata*. We observe that *M. filifolia* has leaves that are more filiform than those of *M. laciniata* and other similar species, including *M. conspicua*, *M. holmgreniorum* (described below), and *M. lagarosa*, which also have thin, pinnate lobes along the narrow rachis of their leaf laminas, but not as narrow as *M. filifolia*. All five of these species, which occur in the southeastern portion of the Colorado Plateau (Fig. 3), are similar in having yellow petals and seed testal cells that have sinuate anticlinal walls. Henry Thompson recognized this entity earlier by annotating herbarium specimens of *M. filifolia* using the specific epithet "navajoa."

Molecular phylogenetic results (Schenk 2009) place *M. filifolia* as sister to the Chihuahuan Desert endemic *M. mexicana* H. J. Thoms. & Zavort., but this relationship has little support. *Mentzelia filifolia* differs from *M. mexicana* in having pinnatisect versus pinnately-lobed laminas, larger flowers, and sinuate versus straight to wavy anticlinal cell walls of the testal cell walls (Fig. 1). We note that the pinnatisect laminas of *M. filifolia* are morphologically most similar to those of *M. laciniata*, *M. lagarosa*, and *M. conspicua*. The lack of support for the relationship of *M. filifolia* and *M. mexicana* in conjunction with the morphological similarities it has to other species begs a more thorough study of the phylogenetic relationships of *M. filifolia*.

Mentzelia holmgreniorum J. J. Schenk & L. Hufford, sp. nov. (Fig. 2C).—Type: USA, Arizona, Apache Co., along US Hwy 60 at side rd to Green's Peak Lookout, 17 mi NW of Springerville, 30°15'N, 109°33'W, 20 Aug 1960, *H. Thompson 3108* (holotype: US; isotype: US).

Habitus singularis erectus; caudex singularis; folia alterna elliptica vel lanceolata, margine pinnatisecta; petala 5, flavidus, spatulata; staminodia extima petaloidea; seminum testa in alam expansa.

Biennial herbs, up to 5 dm tall; taprooted. Main stem erect, straight, lateral branches on distal half of main stem or along the entire main

shoot, lateral branches at acute upward angles to shoot, curved; epidermis pubescent, becoming white, exfoliating with age. Leaves alternate; rosette leaves narrowly to broadly spatulate, petiolate; caulin leaves 42–89 × 11–31.9 mm, rachis width 2.3–3.6 mm; leaves on lower third of main stem oblanceolate to elliptic, margins pinnatisect with 14–20 lobes, 4.6–10.3 mm apart, lobes opposite, lobes strongly angled towards leaf apex, regular, up to 4.9–14.4 mm long with rounded apices, margins revolute; leaves on upper third of main stem lanceolate with non-clasping bases, margins pinnatisect with 12–18 lobes, 6.8–7.9 mm apart, lobes opposite, lobes strongly angled towards leaf apex, regular, up to 4.2–12.4 mm long with rounded or acute apices, margins revolute; pubescent, abaxial surface with greater density of simple grappling-hook, complex grappling-hook, and needle-like trichomes than adaxial surface; adaxial surface with simple grappling-hook and needle-like trichomes. Inflorescence cymose, bract subtending inferior ovary pinnate, 11.7–19.2 × 2.5–6.4 mm. Calyx 6.5–9.4 × 2–2.7 mm, apices acute to attenuate, margins entire. Petals five, yellow, glabrous on abaxial surface, narrowly spatulate, 13.5–18.8 × 5.2–6.6 mm, apex rounded. Androecium yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis not papillate, anther remaining straight following dehiscence; outer whorls of stamens fertile and staminodial, five outermost stamens in median antesepalous positions petaloid, narrowly spatulate, 11.1–16 × 2.7–5 mm, without anther, staminode apex acute; second whorl of stamens all fertile. Gynoecium 3-carpellate, ovary inferior, funnelform, 3 placentae; style 8.4–10.6 mm long, stigmas three. Fruit a capsule, cylindrical, 13.1–14.6 × 5.8–6.9 mm, opening apically by three valves, base tapering, no prominent longitudinal costal ridges. Seeds pale gray with a white wing, lenticular-ovoid, 3.7–3.8 mm long; testa reticulate, seed coat anticlinal cell walls sinuate, central papillae generally 26–51 per cell. Chromosome number $n = 10$ (Christy 1995).

Phenology: Flowering occurs from June to August.

Distribution: Populations occur in sandy washes, along roadsides, and disturbed areas in Apache Co., Arizona, at 1493–2225 m elevation (Fig. 3).

Etymology: We name *M. holmgreniorum* to honor Noel and Patricia Holmgren's contribution to our understanding of *Mentzelia* and their work on the flora of the intermountain West.

Representative specimens: USA. ARIZONA. **Apache Co.**: Vernon, *Bohrer 1100* (ARIZ.); Hwy 60, 1 mi W of Springerville, *Dearen 6482* (ARIZ); 16.6 mi SW of Concho, 14 mi E of Showlow along State Hwy 789 & 61, *H. Thompson 3215* (ARIZ); around the headquarters of Canyon de

Chelly National Monument, T05N R10W S22, *Halse 250* (ARIZ); 10 mi SE of Springerville, White Mountains, *L. Benson 9569* (ARIZ); Greer area, *Schmidt 256* (ARIZ); 4 mi E of Mexican Water, *Shreve 8981* (ARIZ).

Henry Thompson called attention to distinctive collections from Apache Co., Arizona, which he annotated using the nomen nudum "showlowensis." Charlotte Christy (1995) also called attention to these populations, which she annotated with the nomen nudum "pinkavae." We agree with Thompson and Christy that these populations are distinct, and this is supported by phylogenetic results (Schenk 2009), in which an exemplar for *M. holmgreniorum* was recovered in a polytomy that included also the morphologically similar species *M. laciniata*, *M. conspicua*, *M. filifolia*, and *M. lagarosa*. *Mentzelia holmgreniorum* has shorter petals than *M. conspicua*, pinnate rather than the entire ovary bracts characteristic of *M. laciniata*, leaf lobes that are acutely angled toward the leaf apex rather than extending perpendicularly from the axis as characteristic of *M. lagarosa*, and broader lamina lobes and rachis than *M. filifolia*.

***Mentzelia sivinskii* J. J. Schenk & L. Hufford, sp. nov.** (Fig. 4A).—Type: USA, New Mexico, San Juan Co.: 5 mi N of Bloomfield, $36^{\circ}46.750'N$, $107^{\circ}58.876'W$, 18 July 2005, *J. Schenk 1021* (holotype: WS; isotypes: NY, UNM, US).

Habitus singularis erectus; caudex singularis; folia alterna angusta elliptica vel lanceolata, margine pinnata; petala 5, flavidus, spatulata; staminodia absentia; seminum testa in alam expansa.

Biennial herbs, up to 7 dm tall; taprooted. Main stem erect, straight, lateral branches on distal half of main stem or along the entire main shoot, lateral branches at acute upward angles to shoot, straight; epidermis pubescent, becoming white, exfoliating with age. Leaves alternate; rosette leaves narrowly to broadly spatulate, petiolate; cauline leaves $33\text{--}112.2 \times 2.9\text{--}11.4$ mm, rachis width 1–2.9 mm; leaves on lower third of main stem oblanceolate to elliptic, margins pinnate with 18–24 lobes, 3.7–9.3 mm apart, lobes opposite and perpendicularly to leaf axis, regular, up to 0.8–4 mm long with rounded to acute apices, margins revolute; leaves on upper third of main stem elliptic to lanceolate with non-clasping bases, margins pinnate with 6–16 lobes, 3.1–12.7 mm apart, lobes opposite and perpendicularly to leaf axis, regular, up to 1–5.1 mm long with rounded to acute apices, margins revolute; pubescent, abaxial surface with equal or greater density of simple grappling-hook, complex grappling-hook, and needle-like trichomes than adaxial surface; adaxial surface with needle-like and occasionally simple grappling-hook trichomes. Inflorescence cymose, bract subtending inferior ovary entire, $5\text{--}13.4 \times 0.4\text{--}0.8$ mm. Calyx $5.4\text{--}9.3 \times 1.2\text{--}2.9$ mm, apices

acute to attenuate, margins entire. Petals five, light yellow to yellow, glabrous on abaxial surface, narrowly spatulate, $9\text{--}14.7 \times 3.1\text{--}6.4$ mm, apex rounded. Androecium light yellow to yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis not papillate, anther remaining straight following dehiscence; outer whorls of stamens all fertile, five outermost stamens in median anterosepalous positions petaloid, narrowly spatulate, $6.3\text{--}11.5 \times 2.4\text{--}4.9$ mm, with anther occasionally borne on a stalk, filament apex rounded, occasionally with notch; second whorl of stamens all fertile. Gynoecium 3-carpellate, ovary inferior, funnelform, 3 placentae; style 4.6–9.9 mm long, stigmas three. Fruit a capsule, cup-shaped, $8.2\text{--}12.7 \times 5.1\text{--}7.7$ mm, opening apically by three valves, base tapering to rounded, no prominent longitudinal costal ridges. Seeds pale gray to light brown with a white wing, lenticular-ovoid, 2.7–2.8 mm long; testa reticulate, seed coat anticlinal cell walls sinuate, central papillae generally 12–21 per cell. Chromosome number not determined.

Phenology: Flowering occurs from June to August.

Distribution: Populations are narrowly distributed in San Juan Co., New Mexico, at 1524–1816 m elevation (Fig. 3). Plants occur on knolls, slopes, and roadsides in gypsum or brown clay soils.

Etymology: Early collections of *M. sivinskii* were collected by Robert Sivinski, and we name this entity for his contributions to understanding the flora of New Mexico and the diversity of *Mentzelia*.

Representative specimens: USA. NEW MEXICO. San Juan Co.: Jones Mine (abandoned), ca. 2.7 air mi NW of La Plata, $36^{\circ}58'04"N$, $108^{\circ}12'26"W$, *Sivinski 6614* (WS); 27 mi S of the CO border on the NM State Hwy 511, *Kelley 46* (UNM); on old roadbed across dissected highland bordering canyon, T27N R10W S18, SW1/4 of NW1/4, *Lousre 340* (ARIZ).

Schenk (2009) found *M. sivinskii* to be most closely related to *M. integra* and *M. procera* in molecular phylogenetic analyses. *Mentzelia sivinskii* is narrowly distributed in San Juan Co., New Mexico, and it overlaps with the northwestern range of *M. procera*. In contrast, *M. integra* is distributed in the Great Basin, where it is disjunct from its closest relatives. Although the flowers of these three species are similar, the outermost stamens opposite the sepal lobes are fertile in *M. sivinskii* but are staminodial in *M. integra* and *M. procera*. The most distinctive features of *M. sivinskii* compared to its relatives are narrow lobes on leaves and deep sinuses between these lobes, and in these attributes, *M. sivinskii* converges somewhat on leaf attributes of its geographic neighbor *M. laciniata*.

Collections of *M. sivinskii* have been misidentified as *M. multicaulis* (Osterh.) J. Darl. (R.

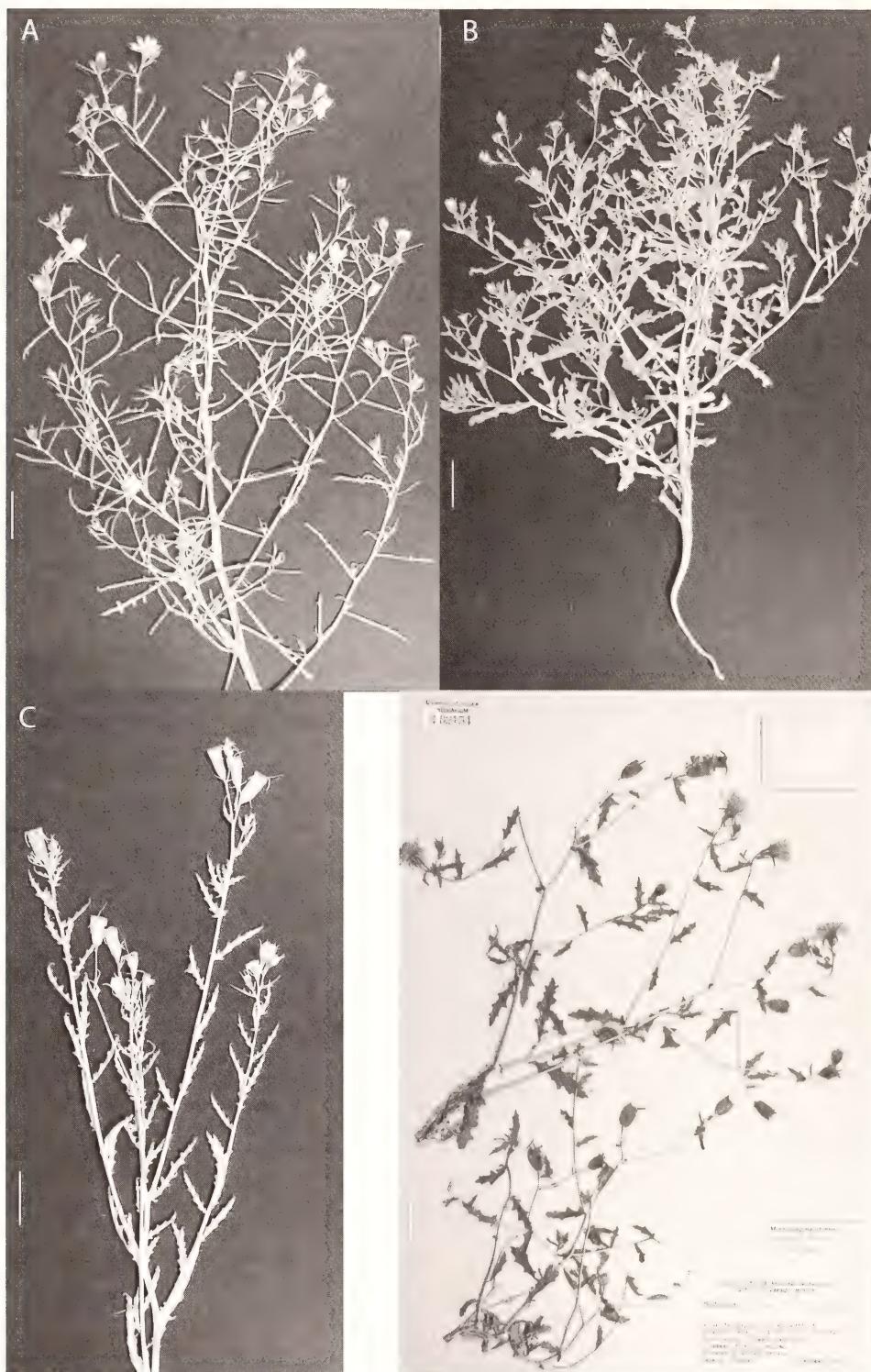


FIG. 4. Type specimens of newly described taxa. A. *Mentzelia sivinskii*, B. *M. longiloba* var. *chihuahuaensis*, C. *M. longiloba* var. *yavapaiensis*, and D. *M. longiloba* var. *pinacatensis*. Scale bars = 3 cm.

TABLE 1. MORPHOLOGICAL STATES OF THE VARIETIES OF *M. LONGILOBA*. MAS = median antesepalous stamens, the outermost stamens opposite sepals. All measurements are in millimeters.

Character	var. <i>longiloba</i>	var. <i>chihuahuensis</i>	var. <i>pinacatensis</i>	var. <i>yavapaiensis</i>
Leaf length	37–112	35–110	35–110	39–71
Leaf width	8.4–24.6	7.4–27.1	5.5–22.0	8.3–19.1
Rachis width	3.3–13.7	2.3–9.0	2.1–7.3	3.5–6.6
Number of lobes	10–28	12–18	8–50	10–24
Lobe length	up to 1.4–6.8	up to 2.3–9	up to 3.3–8.9	up to 2.4–6.5
Petal length	13.3–17.5	11.3–16.3	11.9–19.8	12.6–13.6
Petal width	3.7–6.8	3.1–5.1	4.7–8.9	4.5–5.6
Petal apex	acute to rounded	acute to rounded	rounded	rounded
MAS length	(6.7)10.6–15.5	11.2–15.4	9.7–16.9	11.4–12.8
MAS width	1.9–5.2	2.4–4.0	3.3–5.6	2.9–4.2
MAS staminodial	yes	yes/no	yes/no	no
Capsule length	9.6–16.4	10.0–15.0	7.6–13.2	9.7–15.2
Capsule width	6.0–9.2	5.7–8.3	5.8–8.5	5.7–7.2
Seed length	3.3–4.0	2.9–3.2	2.9–3.4	3.0–3.4
Anticinal walls	sinuate	straight	sinuate	sinuate
Number of papillae	67–106	4–6	26–51	10–21
Distribution	California, Arizona, New Mexico, Texas, Utah, Sonora	Chihuahua	Sonora	AZ

Sivinski, EMNRD-Forestry Division, personal communication) based on the identification key in Darlington (1934). *Mentzelia multicaulis* is, however, distributed only in western Colorado and eastern Utah (Holmgren and Holmgren 2002). Unlike the perennial *M. multicaulis*, which produces multiple aerial branches from a subterranean caudex (Holmgren and Holmgren 2002; Schenk and Hufford 2009), *M. sivinskii* has a single main stem (Fig. 4).

NEW VARIETIES OF *MENTZELIA LONGILOBA*

Josephine Darlington (1934) first recognized *M. longiloba* as a distinct species distributed in eastern Utah and southern California. Although she differentiated *M. longiloba* from *M. multiflora* (Nutt.) A. Gray on the basis of shorter capsules that have acute bases, Felger (1980) treated the two entities as conspecific and recognized *M. multiflora* subsp. *longiloba* (J. Darl.) Felger. Our phylogenetic studies indicated *M. multiflora* s.s. is more closely related to other mentzelias than it is to *M. longiloba* (Schenk 2009). *Mentzelia multiflora* s.s. can be distinguished from *M. longiloba* by its longer capsules (11.2–26.1 mm versus 7.6–16.4 mm), attenuate rather than rounded capsule bases, and entire rather than pinnate prophylls. We recognize *M. multiflora* s.s. as a taxon limited to the eastern side of the Southern Rocky Mountain Front Range, and we present below a new interpretation of the range of *M. longiloba*.

Our phylogenetic analyses identified a set of morphologically and geographically distinct populations in a polytomy with *M. longiloba* s.s. (Schenk 2009). Although these populations can

be distinguished from *M. longiloba* s.s. based on micromorphological states of seed coats, they diverge from it otherwise in largely continuous macromorphological states (Table 1). Given the partially continuous morphological variation of these distinctive populations with *M. longiloba* while having geographical uniqueness, we recognize them as varieties of *M. longiloba*.

Our concept of *M. longiloba* var. *longiloba* is mostly consistent with that of Darlington's (1934) *M. longiloba*, although we recognize additional variation. Based on collections not available to Darlington (1934), we extend the range of *M. longiloba* var. *longiloba* from California and Utah, to include also Arizona, New Mexico, Texas, and northern Mexico. Additionally, we extend the range of morphological variation to recognize longer petals (13.3–17.5 mm) and longer capsules (9.6–16.4 mm).

Among the new varieties of *M. longiloba* we describe below, var. **chihuahuensis** can be distinguished from the others by the straight anticinal walls and 4–6 papillae on the outer pericinal wall of seed coat testal cells versus the sinuate anticinal walls and 10–106 papillae per cell among the other varieties (Table 1, Fig. 5). Variety **yavapaiensis** can be distinguished from var. **pinacatensis** because all stamens, including the petaloid outermost stamens, are fertile, its petals are shorter, and its leaves have a lower maximum number of lobes (Table 1). We distinguish var. **yavapaiensis** from var. *longiloba* primarily by having fewer papillae per outer pericinal wall of seed coat testal cells than the latter. The leaves of var. **pinacatensis** are narrower and its capsules shorter than those of the other varieties (Table 1).

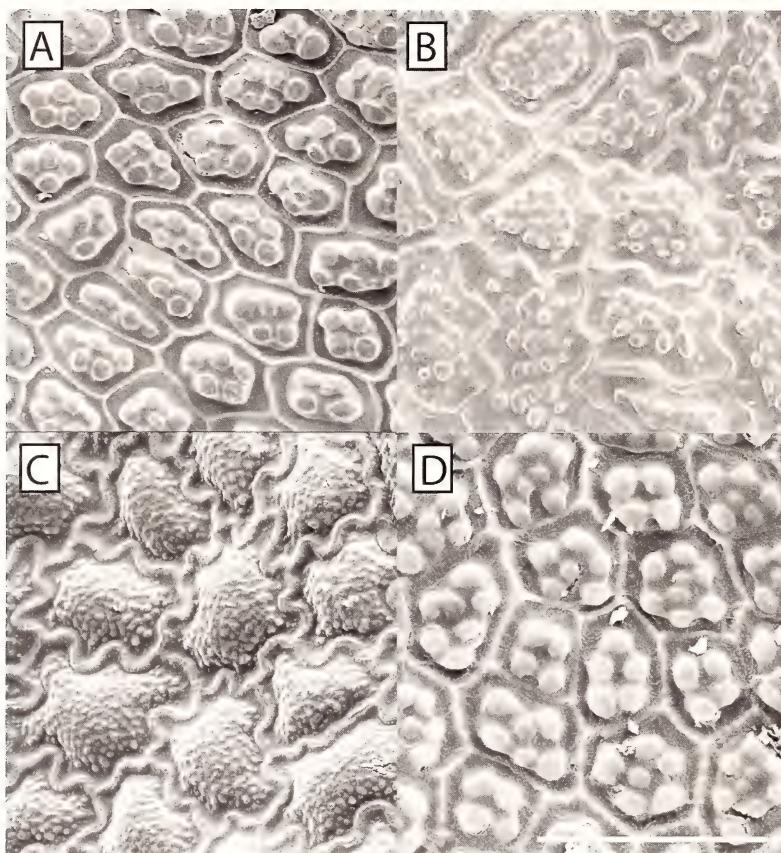


FIG. 5. Scanning electron micrographs of seed coat testal cells. A. *M. longiloba* var. *chihuahuensis*, B. *M. longiloba* var. *yavapaiensis*, C. *M. longiloba* var. *longiloba*, and D. *M. longiloba* var. *pinacatensis*.

Mentzelia longiloba* J. Darl. var. *chihuahuensis

J. J. Schenk & L. Hufford var. nov. (Fig. 4B).—Type: USA, Texas, Brewster Co., Rte 118, S of 898, on W side of rd with E exposure, 30°05.898'N, 103°35.782'W, 1385 m elevation, 7 Aug 2004, J. Schenk 901 (holotype: WS; isotypes: ARIZ, NY, UNM, TEX, US).

Habitus singularis erectus; caudex singularis; folia alterna elliptica vel lanceolata, marginē lobata; petala 5, flavidus, spatulata; staminodia extima petaloidea; seminum testa in alam expansa.

Biennial herbs, up to 5 dm tall; taprooted. Main stem erect, straight, lateral branches on distal half of main stem or along the entire main shoot, lateral branches at acute upward angles to shoot, upwardly curved; epidermis, pubescent, becoming white or gray, exfoliating with age. Leaves alternate; rosette leaves narrowly to broadly spatulate, petiolate; cauline leaves 35–110 × 7.4–27.1 mm, rachis width 2.3–9 mm; leaves on lower third of main stem oblanceolate to elliptic, margins dentate with 12–18 lobes, 8.4–12.5 mm apart, lobes opposite and perpendicular to leaf axis, regular, up to 2.3–9 mm long with rounded to acute apices, margins revolute; leaves

on upper third of main stem lanceolate with non-clasping bases, margins serrate to pinnate with 10 lobes, 6.8–9.4 mm apart, lobes opposite and slightly angled towards leaf apex, regular, up to 2.9–7.5 mm long with rounded to acute apices, margins revolute; pubescent, abaxial surface with greater density of simple grappling-hook, complex grappling-hook, and needle-like trichomes than adaxial surface; adaxial surface with simple grappling-hook and needle-like trichomes. Inflorescence cymose, bract subtending inferior ovary entire to rarely pinnate, 5.2–9.9 × 0.7–2.6 mm. Calyx 5.5–8.8 × 1.9–3.3 mm, apices acute to attenuate, margins entire. Petals five, yellow, glabrous on abaxial surface, narrowly spatulate, 11.3–16.3 × 3.1–5.1 mm, apex acute to rounded. Androecium yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis not papillate, anther remaining straight following dehiscence; outer whorls of stamens fertile and staminodial, five outermost stamens in median antesepalous positions petaloid, narrowly spatulate, 11.2–15.4 × 2.4–4 mm, without anther, staminode apex acute to rounded; second whorl of stamens all fertile. Gynoecium 3-carpellate, ovary inferior, funnel-

form, 3 placentae; style 6.4–9.8 mm long, stigmas three. Fruit a capsule, cup-shaped, 10–15 × 5.7–8.3 mm, opening apically by three valves, base tapering, no prominent longitudinal costal ridges. Seeds light brown with a white wing, lenticular-ovoid, 2.9–3.2 mm long; testa reticulate, seed coat anticlinal cell walls straight, central papillae generally 4–6 per cell. Chromosome number not determined.

Phenology: Flowering occurs from August to November.

Distribution: Populations occur in the Chihuahuan Desert in New Mexico and Texas in the United States and Chihuahua and Coahuila states of northeastern Mexico at 548–1555 m elevation (Fig. 3). Plants occur on sand dunes and along roadsides in dry clay or sandy soils that are often disturbed.

Etymology: *Mentzelia longiloba* var. *chihuahuensis* is named for the Chihuahuan Desert, to which it is endemic.

Representative specimens: MEXICO. CHIHUAHUA. Samalayuca Dunes, ca. 5 miles S of Samalayuca, and ca. 35 mi S of Ciudad Juarez, 31°17'N, 106°30'W, Provance *et al.* 1678 (UCR). COAHUILA. along Rio Grande, just S of Ojo Caliente, river mileage 808.3, 29°11'N, 102°56'W, Hodgson *et al.* 5265 (UCR). USA. NEW MEXICO. Hidalgo Co.: Taylor Draw at Animas Creek in Upper Animas Valley, 0.4 mi N of the jct with the rd over the mountains to Douglas, on Rte 338, T31S R20W S33, Sanders *et al.* 3051 (UCR). TEXAS. Brewster Co.: E of Marathon, across from Housetop Mtns on Hwy 90, on S side of rd with N exposure, 30°12.233'N, 102°57.562'W, Schenk 909, 910 (WS); Route 118, at intersection with Calamity Creek Rd, S of Alpine, 30°10.173'N, 103°35.031'W, Schenk 898, 900 (WS); S-facing road-cut on Hwy 90 just E of Alpine (across from stinking cattle feedlot), 30°22.539'N, 103°36.658'W, Hufford 4311 (WS). Jeff Davis Co.: Route 17, S of Boy Scout camp by a few mi, Davis Mountains, N of Fort Davis, 30°48.954'N, 103°45.869'W, Schenk 897 (WS). Terrell Co.: along Hwy 90, E of Sanderson and Dryden, 1 mi W of Lozier Canyon, 4 mi W of jct with Hwy 1865 (to Pumpville), and ca. 15 mi W of Langtry, 29°54.296'N, 101°49.263'W, Hufford 4312 (WS).

Collections of *M. longiloba* var. *chihuahuensis* are often identified as *M. multiflora*, but their seed coat testal cells can readily distinguish them. Seed coat cells of *M. longiloba* var. *chihuahuensis* have straight anticlinal walls and 4–6 papillae that are centrally located on a raised dome of the outer periclinal wall of each testal cell (Fig. 5), whereas testal cells of *M. multiflora* have sinuate anticlinal walls and 34–48 papillae per cell (Fig. 1). Although the northern portion of the range of *M. longiloba* var. *chihuahuensis* extends into southern New Mexico (Fig. 3), it does not

overlap with the range of *M. multiflora*, which reaches its southern limit in northern New Mexico. The range of *M. longiloba* var. *chihuahuensis* marginally overlaps with the southern range of *M. procera*, which can be differentiated from *M. longiloba* var. *chihuahuensis* by the sinuate anticlinal walls of its seed testal cells (Fig. 1c), more narrow leaves (5.3–14.9 mm vs. 7.4–27.1 mm) with a narrower rachis (1.7–3.9 mm vs. 2.3–9 mm), a wide leaf base, and greater number of lobes (14–26 vs. 12–18).

Mentzelia longiloba* J. Darl. var. *pinacatensis

J. J. Schenk & L. Hufford var. nov. (Fig. 4D).

—Type: MEXICO, Sonora, Pinacate Region, 1.1 km N of Pinacate Peak, 31°47'05"N, 113°29'25"W, 950 m elevation, 13 Oct 1986, R. Felger & G. Joseph 86-432 (holotype: ARIZ; isotypes: ARIZ, RSA).

Habitus singularis erectus; caudex singularis; folia alterna elliptica vel lanceolata, breva, margine lobata; petala 5, flavidus, spatulata; staminodia extima petaloidea; seminum testa in alam expansa.

Biennial herbs, up to 5 dm tall; taprooted. Main stem erect, straight, lateral branches along the entire main shoot, lateral branches at acute upward angles to shoot, upwardly curved; epidermis pubescent, becoming white, exfoliating with age. Leaves alternate; rosette leaves narrowly to broadly spatulate, petiolate; caulin leaves 35–110 × 5.5–22 mm, rachis width 2.1–7.3 mm; leaves on lower third of main stem elliptic, margins dentate to pinnate with 18–50 lobes, 2.9–18.2 mm apart, lobes opposite and perpendicular to leaf axis, irregular or regular, up to 3.3–6.9 mm long with acute apices, margins revolute; leaves on upper third of main stem elliptic to lanceolate with non-clasping bases, margins dentate to pinnate with 8–28 lobes, 2.1–5.5 mm apart, lobes opposite and perpendicular to leaf axis, irregular or regular, up to 1.7–8.9 mm long with acute apices, margins revolute; pubescent, abaxial surface with greater density of simple grappling-hook, complex grappling-hook, and generally with needle-like trichomes than adaxial surface; adaxial surface with simple grappling-hook and needle-like trichomes. Inflorescence cymose, bract subtending inferior ovary entire, toothed, or pinnate, 5.4–15.7 × 0.7–2.8 mm. Calyx 6.7–13.6 × 1.7–3.5 mm, apices acute to attenuate, margins entire. Petals five, yellow, glabrous on abaxial surface, narrowly spatulate, 11.9–19.8 × 4.7–8.9 mm, apex rounded. Androecium yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis not papillate, anther remaining straight following dehiscence; outer whorls of stamens fertile or staminodial, five outermost stamens in median antesepalous positions petaloid, narrowly spatu-

late, $9.7\text{--}16.9 \times 3.3\text{--}5.6$ mm, with or without anther, filament or staminode apex rounded; second whorl of stamens all fertile. Gynoecium 3-carpellate, ovary inferior, funnelform, 3 placentae; style 7.6–11.4 mm, stigmas three. Fruit a capsule, cup-shaped, $7.6\text{--}13.2 \times 5.8\text{--}8.5$ mm, opening apically by three valves, base rounded, no prominent longitudinal costal ridges. Seeds light brown with a white to light brown wing, lenticular-ovoid, 2.9–3.4 mm long; testa reticulate, seed coat anticinal cell walls sinuate, central papillae generally 26–51 per cell. Chromosome number not determined.

Phenology: Flowering occurs from March to April.

Distribution: Populations are distributed in the Pinacate Desert of Sonora, Mexico, at 200–950 m elevation (Fig. 3). Plants occur on slopes in soils composed largely of decomposed volcanic cinder rocks and ash.

Etymology: *Mentzelia longiloba* var. *pinacatensis* is named for the Pinacate Desert, to which it is restricted.

Representative specimens: MEXICO. SONORA. Pinacate Region, ash flat adjacent to N end of Mayo lava flow, 2 April 1989, *Dimmitt s.n.* (ARIZ); ca. 1.8 km NWW of Pinacate Peak, $31^{\circ}46.5'N$, $113^{\circ}30'W$, *Felger et al. 19475* (ARIZ); Pinacate Region, ca. 0.5 km W of Campo Rojo (=Red Cone Camp), $31^{\circ}46'N$, $113^{\circ}27'W$, *Felger et al. 87-56* (ARIZ); lava flow NE of Crater Elegante, $31^{\circ}50'30"N$, $113^{\circ}20'W$, *Fishbein & Meggs 30* (ARIZ); E trail of Pinacate Peak, Sierra Pinacate, NW Sonora, $31^{\circ}45'N$, $113^{\circ}30'W$, 9 Apr 1983, *Sherbrooke s.n.* (ARIZ); Pinacate Mountains, Red Cone Camp, $31^{\circ}47'N$, $113^{\circ}27'W$, 19 Mar 1983, *Soule s.n.* (ARIZ); Sierra del Pinacate, SE of Pinacate Peak, $31.55'N$, $113.25'W$, *Webster 22298* (ARIZ).

The Pinacate region of northern Mexico has been shaped by recent volcanic activity during the Pleistocene to Holocene (Ezcurra et al. 1987), and *M. longiloba* var. *pinacatensis* is one of several endemic taxa that appear to have evolved on its distinctive soils (Felger 1991). Collections of this taxon have been previously identified as *M. longiloba* (or *M. multiflora* subsp. *longiloba*). Variety *pinacatensis* has shorter leaves, more numerous lobes per leaf, narrower petals, petaloid fertile stamens rather than staminodes in outermost androecial positions opposite sepals, and shorter capsules compared to *M. longiloba* var. *longiloba* (Table 1).

Mentzelia longiloba J. Darl. var. *yavapaiensis* J. J. Schenk & L. Hufford var. nov. (Fig. 4C). —

Type: USA, Arizona, Yavapai Co., Juniper Mountains, W of Flagstaff, Cross Mountain Rd., near Hwy I-40, $35^{\circ}11.767'N$, $113^{\circ}18.280'W$, 1576 m elevation, 1 July 2005, *J. Schenk 1011* (holotype: WS; isotype: ARIZ).

Habitus singularis erectus; caudex singularis; folia alterna elliptica vel lanceolata, margine lobata; petala 5, flavidus, spatulata; staminodia extima petaloidea; seminum testa in alam expana; chromosoma noven.

Biennial herbs, up to 7 dm tall; taprooted. Main stem erect, straight, lateral branches on distal half of main shoot, lateral branches at acute upward angles to shoot, upwardly curved; epidermis pubescent, becoming white, exfoliating with age. Leaves alternate; rosette leaves narrowly to broadly spatulate, petiolate; caudine leaves $39\text{--}71 \times 8.3\text{--}19.1$ mm, rachis width 3.5–6.6 mm; leaves on lower third of main stem oblanceolate to elliptic, margins pinnate with 14–24 lobes, 3.1–9.6 mm apart, lobes opposite and slightly angled towards leaf apex, irregular or regular, up to 2.4–6.5 mm long with rounded or acute apices, margins revolute; leaves on upper third of main stem lanceolate with non-clasping bases, margins pinnate with 10–20 lobes, 5–10.2 mm apart, lobes opposite or alternate and slightly angled towards leaf apex, irregular or regular, up to 2.6–5.8 mm long with rounded or acute apices, margins revolute; pubescent, abaxial surface with greater density of simple grappling-hook, complex grappling-hook, and occasionally needle-like trichomes than adaxial surface; adaxial surface with simple grappling-hook and needle-like trichomes. Inflorescence cymose, bract subtending inferior ovary entire, $4.6\text{--}14.5 \times 0.3\text{--}1.1$ mm. Calyx $7.2\text{--}8.1 \times 1.9\text{--}2.3$ mm, apices acute to attenuate, margins entire. Petals five, yellow, glabrous on abaxial surface, narrowly spatulate, $12.6\text{--}13.6 \times 4.5\text{--}5.6$ mm, apex rounded. Androecium yellow, stamens numerous, those of inner whorls shorter than outer whorls, filaments glabrous, anther epidermis not papillate, anther remaining straight following dehiscence; outer whorls of stamens fertile and staminodial, five outermost stamens in median antesepalous positions petaloid, narrowly spatulate, $11.4\text{--}12.8 \times 2.9\text{--}4.2$ mm, without anther, staminode apex acute to rounded; second whorl of stamens all fertile. Gynoecium 3-carpellate, ovary inferior, funnelform, 3 placentae; style 8.8–10.6 mm long, stigmas three. Fruit a capsule, cup-shaped to cylindrical, $9.7\text{--}15.2 \times 5.7\text{--}7.2$ mm, opening apically by three valves, base tapering to rounded, no prominent longitudinal costal ridges. Seeds pale gray with a white wing, lenticular-ovoid, 3–3.4 mm long; testa reticulate, seed coat anticinal cell walls sinuate, central papillae generally 10–21 per cell. Chromosome number $n = 9$ (*H. Thompson 3405* [ARIZ]).

Phenology: Flowering occurs from March to October.

Distribution: Populations are located in Apache, Coconino, Mohave, Navajo, Pinal, and Yavapai counties in Arizona, where they occur in sandy washes and along roadsides at 432–1676 m elevation (Fig. 3).

Etymology: *Mentzelia longiloba* var. *yavapaiensis* is named for Yavapai Co., Arizona, where the type specimen was collected.

Representative specimens: USA. ARIZONA. **Coconino Co.:** Wupatki National Monument, Flagstaff, *Demaree* 43981 (ARIZ). **Mohave Co.:** 4 mi W of Peach Springs, *Kearney & Peebles* 12747 (ARIZ); Hualapai Mountains, SE of Hualapai Mountain Park, 35°05'N, 113°52'W, *Vasek & Clarke HMS-112* (UCR); Tuweep, rim of Grand Canyon, *Cottam* 8594 (ARIZ); along main rd between Wolf Hole and Cottonwood Wash, T38N R15W S36, *Mason & Phillips* 2885 (ARIZ). **Navajo Co.:** Corduroy Canon, 20 mi SW of Show Low along US Hwy 60, *H. Thompson* 3218 (ARIZ); State Rte 77, ca. 11 mi S of Navajo Indian Reservation boundary, 3 mi S of Leroux Wash, T19N R21E, 23 Sep. 1973, *Spaulding s.n.* (ARIZ); near Oraibi, 24 July 1958, *Haskell & Hevly s.n.* (ARIZ); Newberry Mesa N of Winslow, 9 June 1940, *Darrow s.n.* (ARIZ); Winslow, *M. Jones* 4112 (ARIZ). **Pinal Co.:** Casa Grande Ruins National Monument, *D. Turner & DeKoker* 59 (ARIZ); Pinal Mountains, *Kearney et al.* 6364 (ARIZ); Sacaton Agency, *Gilman* 220 (ARIZ); San Pedro Valley, 4.9 mi SE of Main St in San Manuel via rd to San Pedro River, dissected lower Bajada ca. 1 mi W of river, T10S R18E, *Burgess & Burgess* 5950 (ARIZ); W

of Gila Butte beneath and around new overpass bridge, *S. Adams* 34 (ARIZ). **Yavapai Co.:** about 80 mi SE of Kingman, *Kearney & Peebles* 12586 (ARIZ); Antelope Creek, S Weaver Mountains, Yarnell 7.5 Quad, T10N R04W S19 NW1/4, *Butterwick & Hillyard* 6871 (ARIZ); Black Hills, 5 mi E of Cherry, 34°35'26"N, 111°59'46"W, *Helmkamp* 7-17 (UCR); Lynx Lake area of Prescott National Forest, 4.8 mi S of Hwy 69 on 197, ca. 6 mi SE of Prescott, *L. & S. Landrum* 5591 (UCR); Page Springs, *Demaree* 44336 (ARIZ); Prescott National Forest, 7.8 mi SW of Prescott on Hwy 89, 34°27'N, 112°32'W, *Vasek & Clarke* 660911-54 (UCR); SW of Prescott, 2 mi SW of Kirkland Junction, *H. Thompson* 3405 (ARIZ).

Collections of *Mentzelia longiloba* var. *yavapaiensis* have often been determined as *M. multiflora*, which is consistent with Darlington's (1934) broad treatment of the latter species. The phylogenetic results of Schenk (2009) demonstrated that Darlington's (1934) concept of *M. multiflora* encompassed polyphyletic lineages. *Mentzelia longiloba* var. *yavapaiensis* is more closely related to *M. longiloba* var. *pinacatensis* than it is to *M. multiflora* s.s. (Schenk 2009). *Mentzelia longiloba* var. *yavapaiensis* has short, cup-shaped capsules in contrast to the long, cylindrical capsules of *M. multiflora* s.s.

IDENTIFICATION KEY TO *MENTZELIA* SECTION *BARTONIA* FOR TAXA DISCUSSED ABOVE

1. Plants with multiple stems that arise from a subterranean branching caudex, plants often forming rounded tufts *M. multicaulis*
- 1' Plants with a simple caudex (=single main stem, or multiple stems that arise from a single region) at or above the soil surface
 2. Petals pubescent on abaxial surfaces
 3. Most leaves above the base of plant shallowly lobed with rounded to acute margins or entire, especially on the secondary and tertiary branches; outer stamens opposite each sepal with anther; w. CO *M. marginata*
 - 3' Most leaves (except prophylls) pinnately lobed on all orders of branches, lobes acute; outer stamens opposite each sepal with/without anther; w. CO, AZ, NW, UT
 4. Lateral branches at acute angles to the main stem and extend to near the distal end of the plant (creating a candelabrum profile with a flat to round top); capsules 6–16 × 5–7.3 mm; AZ, CO, NM, UT *M. croniquistii*
 - 4' Lateral branches perpendicular or acutely angled to main shoot, generally of nearly equal lengths, lateral branching often dense (creating a cylindrical profile); capsules 5–9 × 3.7–6.5 mm; Montrose and San Miguel counties, CO *M. paradoxensis*
 - 2' Petals glabrous on abaxial surfaces
 5. Leaves along main stem pinnatisectly lobed
 6. Petals 27 mm or longer *M. conspicua*
 - 6' Petals less than 26 mm long
 7. Petals 13 mm long or less and floral bracts subtending ovaries pinnate *M. lagarosa*
 - 7' Petals greater than 13 mm long and floral bracts subtending ovary entire to pinnate
 8. Lamina lobes filiform, 1.4 mm wide or less, lobes up to 17 mm long *M. filifolia*
 - 8' Lamina lobes narrow, greater than 1 mm wide, lobes up to 14.4 mm long
 9. Entire bracts subtending ovaries; leaf lobes slightly angled toward distal tip of leaf or perpendicular to leaf axis; NM and CO *M. lacinata*
 - 9' Pinnate bracts subtending ovaries; leaf lobes strongly angled toward distal tip of leaf; AZ *M. holmgrenorum*
 - 5' Leaves along main stem entire, dentate, serrate, to pinnately lobed
 10. Largest trichomes of leaves with ring-like pedestals of pearly white cells; leaf lobes angled on proximal side of lobe, perpendicular on distal side of lobe; stem epidermis generally glabrous or occasionally pubescent, leaf lobes few, generally less than 12 *M. integra*

10' Leaf trichomes of leaves without ring-like pedestals of pearly white cells; leaf lobes with isometrically angled sides; stem pubescent, leaf lobes many, generally greater than 6

11. Anticinal walls of testal cells straight

12. Capsules cup-shaped (less than or equal to twice as long as wide)

13. Capsules 9.6–19 mm long; 4–6 papillae per testal cell *M. longiloba* var. *chihuahuensis*

13' Capsules 5.3–13 mm long; 8–12 papillae per testal cell. *M. mexicana*

12' Capsules cylindrical (greater than twice as long as wide). *M. pumila*

11' Anticinal walls of testal cells sinuate

14. Seed pericinal wall with 67 or more papillae per cell *M. longiloba* var. *longiloba*

14' Seed pericinal wall with 68 or fewer papillae per cell

15. Outermost stamens opposite sepal lobes with anther

16. Leaf rachis 1–2.9 mm wide *M. sivinskii*

16' Leaf rachis 3.5–6.6 mm wide *M. longiloba* var. *yavapaiensis*

15' Outer stamens opposite each sepal lobes generally staminodial

17. Capsules 5.3–13 mm long; plants occur on volcanic soils *M. longiloba* var. *pinacatensis*

17' Capsules 9.6–26 mm long; plants occur on loam soils

18. Upper leaf rachis 1.7–3.9 mm wide; capsules 5.2–7.3 mm wide. *M. procera*

18' Upper leaf rachis 2.1–13.7 mm wide; capsules 5.1–9.2 mm wide. *M. multiflora*

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BRODIAEA MATSONII (ASPARAGACEAE: BRODIAEOIDEAE) A NEW SPECIES FROM SHASTA COUNTY, CALIFORNIA

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ABSTRACT

A newly recognized endemic species, *Brodiaea matsonii*, is described. This highly localized species is restricted to a single extended population along Sulphur Creek, in Redding, Shasta County, California. *Brodiaea matsonii* is a diploid species ($n = 6$) closely related to the more widespread *B. minor*, a polyploid species ($n = 12, 24$), from which it differs by the slightly smaller pink flowers and by its habitat parameters. *Brodiaea matsonii* grows from cracks and crevices in bedrock along an intermittent stream within foothill woodland.

Key Words: Asparagaceae, *Brodiaea*, California, endemism, new species.

In 1993, Gary Matson discovered an unusual pink-flowered brodiaea growing along Sulphur Creek, north of Redding, California. Initial attempts to identify the plants suggested a relationship with *Brodiaea pallida* Hoover, a species known from only three other populations in Calaveras and Tuolumne counties, a disjunction of ca. 335 km. Mr. Matson collected corms from the population and gave them to Dean Taylor, an expert on California's rare plants. Dr. Taylor, in turn, presented me with a pot of the corms in 2007 at a symposium sponsored by the Northern California Botanists, where I gave a presentation on brodiaeas.

In late May, when the plants bloomed, I recognized that they were not *B. pallida* but morphologically were more similar to *B. minor* (Benth.) S. Watson. Further investigations of the Sulphur Creek population, including field surveys, morphological measurements, and chromosome counts show that the population is sufficiently distinct to warrant recognition at species rank.

TAXONOMIC TREATMENT

***Brodiaea matsonii* R. E. Preston, sp. nov.** (Fig. 1).—Type: USA, California, Shasta Co., Redding, on S side of Keswick Dam Rd, 0.4 mi NE of its junction with Quartz Hill Rd, along W Branch of Sulphur Creek; 40°37'13"N, 122°25'25"W, elev. 700 ft, 24 Jun 2009, R. E. Preston 2689 (holotype: DAV; isotypes: JEPS, MO, NY, RSA, US).

Paratypes: USA, CALIFORNIA. **Shasta Co.:** Redding, Upper Sulphur Creek, D. W. Taylor s.n. (JEPS); Redding, along Sulphur Creek, S of Keswick Dam Rd crossing, 04 Jun 2007, R. E. Preston 2548 (DAV); west fork of Sulphur Creek, 04 Jun 2007, R. E. Preston 2547 (JEPS).

Differet a *B. minor* perianthio roseo, costis abaxialibus viridibus, et lobis apicem versus et costis adaxialibus saepe erubescentibus.

Corm with coarse fibrous coat, 1–10 cm below ground level; leaves 2–5, subcrescent-shaped in cross-section, less than 15 cm long; peduncle slender, 10–25 cm tall, pedicels less than 36.5 mm long; perianth 17.4–26.7 mm long, tube urceolate, 6.8–9.4 mm long, lobes ascending, 10.6–17.5 mm long, outer oblong, acute, 3.0–4.2 mm wide, inner oblanceolate, rounded, 3.6–5.2 mm wide, white to pink, tips and abaxial mid-ribs rose, adaxial mid-ribs green; staminodes 6.2–8.5 mm long, erect and approximate to stamens, lanceolate, white, margin entire, involuted; stamens 4.8–6.4 mm long, filament 2.0–2.8 mm long, tapered to wider base, narrowly winged laterally, anther 4.0–5.1 mm long, linear, tips of anther lobes erect with V-shaped notch between; ovary obovate, 3.8–5.6 mm long, style 6.5–9.2 mm long, slightly wider near apex, ovules 5–8 per locule; fruit a loculicidal capsule, ellipsoidal, 5–6 mm long, 3 mm wide, valve apex acute; seeds black, ovoid to rhomboid, finely striate, 1–1.5 mm long.

Chromosome number $n = 6$ (Fig. 2). The chromosome count was performed on root tip cells from corms collected with R. E. Preston 2548 (DAV) (A. Diebold, University of Missouri-Columbia, personal communication).

The species is named for its discoverer, Gary Matson (1949–1999), horticulturalist and founder of the Redding Arboretum (Howe et al. 2000). I suggest “Sulphur Creek brodiaea” as the common name.

DISTRIBUTION, CONSERVATION, AND ECOLOGY

Sulphur Creek brodiaea is restricted to a single occurrence in Shasta Co., California. The species is among the rarest taxa in California, consisting



FIG. 1. *Brodiaea matsonii*. a) Lateral view of inflorescence; b) lateral view of flower; c) oblique view of flower; d) top view of flower.

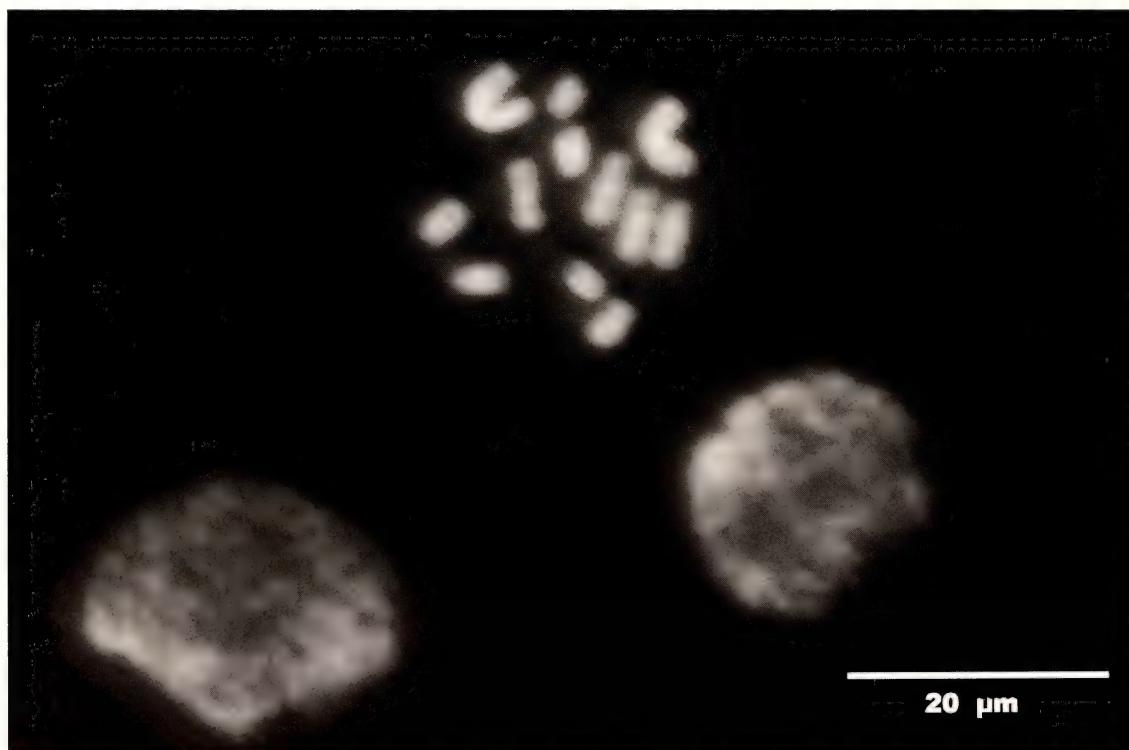


FIG. 2. Chromosomes of *Brodiaea matsonii* from root tip cells (based on R. E. Preston 2548 [DAV]), $2n = 12$ (photograph provided by A. Diebold, University of Missouri-Columbia).

TABLE 1. COMPARISON OF FLORAL CHARACTERS FOR *BRODIAEA MINOR*, *B. NANA*, AND *B. MATSONII*. Measurements were made on fresh material, from one flower per plant, from the type locality of *B. matsonii*, from 20 populations of *B. minor*, and from 16 populations of *B. nana*. Measurements in mm.

Character	<i>Brodiaea nana</i> (n = 170)		<i>Brodiaea minor</i> (n = 204)		<i>Brodiaea matsonii</i> (n = 24)	
	mean	range	mean	range	mean	range
Perianth tube	7.3	5.0–9.0	8.6	6.5–11.5	8.0	6.8–9.4
Perianth lobes	14.3	10.0–21.0	15.0	9.8–20.5	13.5	10.6–17.5
Width, inner lobes	5.2	4.0–8.0	4.7	3.0–7.0	4.5	3.6–5.2
Width, outer lobes	3.8	3.0–5.0	3.7	2.8–5.0	3.6	2.9–4.2
Staminode	7.2	6.0–9.0	9.1	6.2–12.5	7.6	6.2–8.5
Filament	1.4	1.0–2.0	2.4	1–4.2	2.3	2.0–2.8
Anther	4.0	3.0–5.0	5.2	3.5–7.0	4.5	4.0–5.1
Stamen	4.4	3.5–5.2	6.4	4.5–9.0	5.8	5.0–6.6
Ovary	3.5	2.2–5.0	4.9	3.2–7.0	4.5	3.8–5.8
Style	5.3	4.0–7.5	8.8	6.0–12.0	7.9	6.5–9.2
Ovule number	22.5	12–33	17.3	12–24	20.4	15–24

of only a few hundred individuals scattered along a 1.6 km reach of stream channel. The population grows from cracks and crevices in bedrock along the banks and on small rocky islands within the channel of Sulphur Creek, an intermittent stream occurring within foothill woodland. The canopy is characterized by *Quercus douglasii* Hook. & Arn., *Q. wislizeni* A. DC., and *Pinus sabiniana* Douglas, with a shrub understory of *Ceanothus cuneatus* (Hook.) Nutt., *Arctostaphylos viscida* C. Parry, and *Toxicodendron diversilobum* (Torr. & A. Gray) Greene. Associated species include *Sidalcea hirsuta* A. Gray, *Centaurium venustum* (A. Gray) Robinson, and *Holozonia filipes* (Hook. & Arn.) Greene. The Sulphur Creek watershed lies in the region where the Klamath Range, with its predominantly metamorphic geology, intergrades with the predominantly volcanic Cascade Range Foothills. Soils in the area, mapped as Auburn clay loam (Klaseen and Ellison 1974), are formed in material weathered from amphibolite schist, which outcrops extensively along this section of the stream. The elevation ranges from 195 to 215 m above mean sea level.

PHENOLOGY

Like all brodiaeas (Niehaus 1971), Sulphur Creek brodiaea forms corms that are dormant in the soil during the summer drought. New leaves emerge soon after the start of the rainy season, generally in October or November. Similar to the process described for *Triteleia laxa* Benth. (Han et al. 1994; Schlising and Chamberlain 2007), the plants spend the next six months or so producing a new main corm and one to many small offsets. Blooming occurs in late May and June, generally two to three weeks later than populations of *B. minor* in the Redding area. Seed set follows soon after, and all above-ground parts wither and dry during the summer dormant period.

TAXONOMIC RELATIONSHIPS

The genus *Brodiaea* Smith remains a valuable resource for systematic and ecological investigation, despite having been monographed twice (Hoover 1939; Niehaus 1971). Recent treatments of *Brodiaea* recognized 14 species and eight subspecies (four species each with two subspecies), most of which are entirely restricted to the California Floristic Province (Niehaus 1971; Keator 1993; Pires 2002). Clarification of some species circumscriptions (Preston 2006a, b) and new species descriptions (Preston 2006b; Chester et al. 2007) have altered these totals, and the forthcoming second edition of The Jepson Manual will recognize 18 species, two of which have two subspecies apiece (Pires and Preston in press). The description of *Brodiaea matsonii* brings the total number of currently recognized *Brodiaea* taxa to 21, and additional morphometric and phylogenetic studies currently underway are likely to raise that total by several more species.

Brodiaea matsonii appears to be most closely related to *B. nana* Hoover, *B. minor*, and *B. pallida*, based on the morphological similarities between them. The flowers of *B. matsonii* are slightly smaller, on average, than *B. minor*, and they are somewhat intermediate in size between *B. minor* and *B. nana* (Table 1). However, the shape of the stamens and staminodes are closer in all respects to those of *B. minor*, rather than *B. nana* or *B. pallida* (see Figure 1 in Preston [2006a] for comparison of *B. minor* and *B. nana*, and Hoover [1938] for a discussion of *B. pallida*). The main morphological difference between *B. matsonii* and *B. minor* is the pink (vs. blue-violet) flowers. *Brodiaea* species typically have violet flowers, and plants with pink flowers, while not unknown, are unusual. *Brodiaea rosea* (Greene) Baker was originally recognized and described on the basis of its pink flowers. *Brodiaea californica* Lindl. has several pink-flowered populations in

the Battle Creek/Paynes Creek watershed in Tehama and Shasta counties (Rowntree 1936) and at least two populations of *B. sierrae* R. E. Preston have individuals with pink flowers (personal observation; G. Hartwell, Paradise, CA, personal communication). Although pink-flowered cultivars of the latter two species have been named (Burbank 1941), intraspecific taxa have not been proposed for either species on the basis of flower color.

All four of these species are characterized by small flowers (generally <2.5 cm long) with a perianth tube narrowed above the ovary. The urceolate perianth tube appears to be a synapomorphy, as the perianth tube is campanulate or funnel-shaped in all other *Brodiaea* species. Hoover (1939) proposed a series of intrageneric groups of species he felt were related, based primarily on morphological grounds, and he placed *B. nana*, *B. minor*, and *B. pallida* along with *B. stellaris* S. Watson in an informal Section "Stellares". Niehaus (1971) later added *B. insignis* (Jeps.) Niehaus to this group. However, *B. stellaris* and *B. insignis* lack an urceolate perianth tube and possess other morphological differences that indicate that they are probably not closely related to the other species included in section "Stellares". Reliance on morphological data alone has proved of limited usefulness in resolving relationships between and among *Brodiaea* species, and further work is needed.

Because *B. matsonii* consists of a single population and is morphologically similar to *B. minor*, what is the basis for recognizing *B. matsonii* at species rank and not just as a variety or subspecies of *B. minor*? A review of species circumscription within *Brodiaea* provides the context needed to justify this decision.

Taxonomic circumscriptions within *Brodiaea* traditionally have been grounded on the morphological species concept. Species have generally been distinguished on the basis of discrete differences in the shape of the floral parts, whereas taxa delineated on the basis of size differences or the relative position of floral parts have been treated as varieties or subspecies. Unfortunately, all *Brodiaea* species are superficially similar, and determining diagnostic characters among species based primarily on floral characters can be difficult, especially when using pressed specimens (Smith 1811; Greene 1886; Hoover 1939). Historically, *Brodiaea* has been much more broadly circumscribed, and the common name "brodiaea" is still applied to species now segregated among several genera, including *Dichelostemma* Kunth and *Triteleia* Dougl. ex Lindl. Although *Brodiaea* appears closely related to *Dichelostemma*, *Triteleia* appears to be only distantly related (Pires and Sytsma 2002). In addition, the presence of umbels, corms, and other morphological similar-

ties between *Brodiaea* and other lilioid geophytes has made higher order classifications difficult, and *Brodiaea* has been placed variously in Liliaceae, Amaryllidaceae, Alliaceae, and Themidaceae (Hoover 1939; Keator 1989; Niehaus 1971, 1980; Fay and Chase 1996). The most recent phylogenetic classification based on molecular data, places *Brodiaea* and relatives with the Asparagaceae in the subfamily Brodiaeoideae (Chase et al. 2009).

Hoover (1939) epitomized the traditional, morphological approach to species circumscriptions in *Brodiaea*. Hoover was familiar with the concepts of ecotypes and ecological plasticity, invoking these ideas to explain some of the intraspecific variation that he observed in *Brodiaea*, although he did not apply ecological information to inform his taxonomic treatment. He was also limited by the lack of cytological data for *Brodiaea* species. Hoover recognized ten *Brodiaea* species, six of which exhibited minimal intraspecific variation. He reduced four other previously-described species to varieties, citing morphological intermediacy as the basis for his changes in rank. He reduced *B. nana* to a variety of *B. minor*, stating that the two taxa intergraded completely. He treated *B. leptandra* Greene as a variety of *B. californica*, stating that he could find few morphological differences between the two taxa. He recombined *B. terrestris* Kellogg as *B. coronaria* (Salisb.) Engl. var. *macropoda* (Torr.) Hoover, stating that the primary difference between *B. terrestris* and *B. coronaria* was the length of the scapes and pedicels, and that the floral morphology was nearly identical. He treated *Brodiaea rosea*, a rare serpentine endemic known from only a few locations in Lake, Glenn, and Colusa counties as a variety of *B. coronaria*, downplaying the morphological differences between them. Hoover also extended the morphological species concept to brodiaeas in the broad sense. He reduced *Triteleia modesta* H. M. Hall Hoover and *T. leachiae* M. Peck Hoover to varieties (of *T. crocea* Greene and *T. hendersonii* Greene, respectively), noting that the varieties differed morphologically in only minor aspects from the typical forms, except for flower color (Hoover 1941). Hoover later took an approach more in line with the biological species concept (Mayr 1963; Grant 1981), re-elevating *B. leptandra* to species rank on the basis of reproductive isolation, despite its morphological similarity to *B. californica* (Hoover 1955). He also proposed raising morphologically similar varieties of *T. ixoides* Greene to species rank on the basis of genetic isolation through ecological and geographic separation (Hoover 1955).

Niehaus (1971) employed a multifaceted approach to try to get beyond the morphologically-based species concept that limited Hoover's understanding of species' boundaries and the

evolutionary relationships among the species. He attempted to incorporate multiple data sources, including morphology, anatomy, cytology, flavonoid chemistry, hybridization studies, geography, and ecology, to circumscribe *Brodiaea* species. Niehaus' treatment was in accord with the biosystematic species concept (Grant 1981), in which species are defined by reproductive isolation as a consequence of genetic or ecological factors, or both. Niehaus agreed with Hoover's acceptance of *B. leptandra* at species rank, citing differences in morphology, chromosome number, range, habitat, and flowering phenology that distinguished it from *B. californica*. He similarly restored *B. coronaria* var. *macropoda* to species rank (*B. terrestris*) based on morphology, distribution, and chromosome number. He also recognized *B. nana* at species rank, distinguished from *B. minor* on the basis of chromosome number, distribution, and habitat (albeit as *B. minor* and *B. purdyi* Eastw., respectively, as Niehaus had difficulty circumscribing the two species for other reasons [Preston 2006a]).

Niehaus was not entirely consistent in his approach and maintained several subspecies despite noting differences in morphology, chromosome number, and distribution from the typical subspecies. He maintained *B. coronaria* subsp. *rosea* (Greene) Niehaus, although he noted that it was a serpentine endemic with a highly restricted range. He also recognized octoploid ($n = 24$) populations of *B. terrestris* as subsp. *kernensis* (Hoover) Niehaus, despite substantial morphological differences and non-overlapping ranges with hexaploid ($n = 18$) subsp. *terrestris*. He described polyploid ($n = 20$) populations of *B. elegans* Hoover as subsp. *hooveri* Niehaus, even though differences in staminode morphology and distribution distinguish them from $n = 8$ and $n = 16$ populations.

Following the traditional, morphologically-based species concept, *B. matsonii* might not warrant recognition at species rank. However, based on the biosystematic species concept, *B. matsonii* does appear to warrant recognition at species rank. It appears to be reproductively isolated from *B. minor* by a combination of factors, including chromosome number, habitat preference, flowering phenology, and allopatry.

Although *B. matsonii* is morphologically similar to *B. minor*, they have different chromosome numbers. The base chromosome number in *Brodiaea* is $n = 6$; the majority of taxa are polyploid with $n = 12, 18$, and 24 , although *B. elegans* is diploid, having $n = 8, 16$, and 20 cytotypes (Johansen 1932; Burbank 1941; Niehaus 1971). *Brodiaea matsonii* is a diploid, along with seven other species including *B. nana* and *B. pallida*. In contrast, *B. minor* appears to consist of a complex of polyploid populations, with populations at lower elevations in the Sierra Nevada

and Cascade Range foothills reported to be octoploid ($n = 24$) and populations at higher elevations in the Sierra Nevada reported to be tetraploid ($n = 12$) (Niehaus 1971). *B. matsonii* appears to be genetically isolated from *B. minor*, therefore, as hybrids between *Brodiaea matsonii* and *B. minor* would not be expected to be fertile. Niehaus (1971) found that interspecific hybrids had reduced seed set and reduced pollen fertility, and he stated that few interspecific hybrids were known where *Brodiaea* species occurred sympatrically.

Traditionally, cytotypes that lack clear differences in morphology, ecology, or distribution have not been recognized as separate taxa, and this approach has also been followed for *brodiaeas*, both in the narrow and broader sense. Niehaus (1971) acknowledged that several *Brodiaea* species consisted of cytotypes with two or more ploidy levels but declined to recognize taxa based on chromosome number unless there was a clear morphological boundary between them. Keator (1968) found that *Dichelostemma capitatum* (Benth.) Alph. Wood consisted of multiple cytotypes but was unable to identify morphological or ecological differences between them. Similarly, Barkworth (1977) studied polyploidy populations of *Triteleia douglasii* Watson and found no consistent morphological characteristics that could be used to recognize intraspecific taxa. In the case of *B. matsonii*, however, flower color and ecology clearly distinguish it from *B. minor*.

Brodiaea matsonii has very different habitat parameters than *B. minor*. The association of *B. matsonii* with ephemeral stream habitat is very rare within *Brodiaea*. *Brodiaea pallida* similarly occurs along intermittent streams; the population along Sawmill Creek in Calaveras Co. also occurs in blue oak-foothill pine woodland on outcrops of amphibolite schist within the stream channel and along the banks (personal observation). In southern California, *B. filifolia* S. Watson, which generally grows in grasslands and on vernal pool margins, rarely grows from cracks and crevices in bedrock along stream banks (T. Chester, Fallbrook, CA, personal communication). In contrast, *B. minor* occurs across a wide range of habitats, including grassland, vernal pool, seep, meadow, and chaparral, often on substrates of volcanic origin, but also on serpentine and gabbro. However, none of the known populations of *B. minor* occur along streams; if any do so, they must be extremely uncommon. Populations of *B. minor* in Redding, some of which are less than a mile from the occurrence of *B. matsonii*, occur in and adjacent to vernal pools on old alluvial terraces, generally where a hardpan is present. *Brodiaea nana* is also not known to occur along streams, but like *B. matsonii* and *B. pallida*, *B. nana* is associated with a much narrower range of habitats. It is

found primarily in vernal pools, although it also occurs in grassland on thin soil overlying bedrock, where soils become waterlogged following precipitation.

Vernal pools and intermittent streams are both seasonal wetland habitats, having saturated soils during the winter rainy season but drying down during the summer drought. Vernal pools occupied by *B. nana* and *B. minor* typically dry down by mid-April, whereas the intermittent streams occupied by *B. matsonii* and *B. pallida* remain wet until mid-May or later. This extended hydroperiod is reflected in these species flowering phenology. *Brodiaea nana* and *B. minor* populations that occur in vernal pool terrain bloom in April and early May, whereas *B. matsonii* and *B. pallida* populations bloom in late May and early June. Although flowering date in *Brodiaea* species is ecologically plastic with respect to annual variation in spring temperatures and rainfall (Niehaus 1971), the later blooming dates of *B. nana* and *B. pallida* appears to have a genetic basis as well, because both *B. matsonii* and *B. pallida* bloom later than *B. nana* and *B. minor* under common garden conditions (personal observation).

Recent studies based on molecular data have proved useful for understanding relationships within the Brodiaeoideae and may point a way towards resolving species relationships within *Brodiaea* (Pires and Sytsma 2002). A phylogenetic analysis of *Brodiaea* and *Dichelostemma* based on DNA sequences is currently underway that may help to interpret morphological characters and to identify the origin of polyploid lineages, especially those involving cryptic cytotypes. Preliminary results based on ITS sequences indicate that *B. matsonii* is grouped with a clade that is basal to the clades containing *B. minor* and *B. nana* (A. Diebold, University of Missouri-Columbia, personal communication). If that relationship is confirmed by the full analysis, then it would add further support to the recognition of *B. matsonii* at species rank.

Key to the *Brodiaea* Species with the Perianth Narrowed Above the Ovary

- 1a. Staminodes erect to spreading, margins strongly inrolled; stamens narrowly notched at apex, lacking prominent papillae abaxially; filaments winged laterally, T-shaped in cross-section.
 - 2a. Perianth violet, outer mid-ribs red-violet *B. minor*
 - 2b. Perianth pink, outer midribs green, lobe tips and upper inner midribs often rose-pink *B. matsonii*
- 1b. Staminodes erect, margins not to slightly inrolled; stamens broadly V-shaped at apex, with prominent abaxial papillae; filaments winged abaxially, V- or Y-shaped in cross section.
 - 3a. Perianth lobes paler towards the base; perianth tube slightly narrowed above the

ovary; staminodes as broad as or broader than the outer perianth lobes *B. pallida*

3b. Perianth color uniform; perianth tube strongly narrowed above the ovary; staminodes narrower than outer perianth lobes *B. nana*

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HOWELLANTHUS DALESIANUS, RECOGNITION OF A NEW GENUS AND SPECIES IN TRIBE PHACELIEAE (BORAGINACEAE)

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ABSTRACT

Howellanthus (Constance) Walden and R. Patt. is recognized as a new genus, containing a single species **H. dalesianus** (J. T. Howell) Walden and R. Patt., based on morphological evidence. **Howellanthus dalesianus** (Boraginaceae) is a small perennial herb, endemic to northern California and restricted to ultramafic soils. The species was first collected in 1936 by Ella Dales Cantelow and Herbert Clair Cantelow, described by John Thomas Howell as *Phacelia dalesiana* J. T. Howell, and later placed in the monotypic *Phacelia* subg. *Howellanthus* by Lincoln Constance.

Key Words: Boraginaceae, *Howellanthus*, Hydrophyllaceae, Hydrophyloideae, *Phacelia*, Phacelieae, serpentine.

Phacelia dalesiana J. T. Howell was first described in 1937, and named in honor of Ella Dales Miles Cantelow, a long-time friend and correspondent of John Thomas Howell (Campbell n.d.; Howell 1954–1955, 1955, 1955–1957). Ella Dales Cantelow, with her husband, Herbert Clair Cantelow, collected specimens on a trip to the Scott Mountains (Siskiyou Co., California) in 1936. A duplicate was sent to Howell at the California Academy of Sciences for identification, and the “remarkable new phacelia” piqued his interest sufficiently to request an expedition to collect mature fruiting material (Fig. 1) (Cantelow 1937–1940; Howell 1937). The following year Howell and Alice Eastwood traveled to Scott Mountain, guided by the Cantelows, to collect the type specimen. Howell returned again to Scott Mountain in July to collect additional material with mature fruit for the description, and published the new taxon (Howell 1937).

Constance (1953) erected the monotypic subg. *Howellanthus* ($n = 8$) to contain the distinct species (see Constance 1953, p. 201 for scientific illustration), based upon chromosome number differences and taxonomic revisions of infrageneric divisions in *Phacelia* (Cave and Constance 1942, 1944, 1947, 1950; Constance 1949, 1950, 1951). The subgenus has since remained monotypic in treatments of the genus, separated from subg. *Phacelia* ($n = 11$) and subg. *Cosmanthus* ($n = 9$) (Constance 1963; Constance and Chuang 1982; Halse et al. 1993; Ferguson 1998; Garrison 2007).

Phacelia dalesiana has been considered a paleoendemic due to several factors: the systematic isolation of the taxon within *Phacelia*; a hypothesized relictual lineage within Hydrophy-

loideae; and the ecologic specialization on ultramafic substrate, although it lacks the high ploidy level characterizing other paleoendemics (Constance 1953; Favarger and Contandriopoulos 1961; Stebbins and Major 1965). It occurs in the Siskiyou–Trinity mountains, an area of high concentration of Arcto–Tertiary relictual species (Stebbins and Major 1965).

The strongest argument to retain the taxon within *Phacelia* has been common, shared characters between species across several infrageneric divisions in the genus: the scorpioid cyme, although few flowered, lax and axillary from a basal rosette in *P. dalesiana* (Figs. 2 and 3); presence of interstaminal corolla scales (Fig. 4), modified in subg. *Cosmanthus* or absent in sect. *Whitlavia* and sect. *Gymnobothrys*; deeply parted style, which can be lobed in some species of the genus; entire leaves and perennial habit; and $n = 8$, shared with *P. stebbinsii* Constance and Heckard, *P. marcescens* Eastw. ex J. F. Macbr., *P. glabra* Nutt., and *P. quickii* J. T. Howell. However, these characters are also shared to varying degree with *Draperia* Torr., *Hesperochiron* S. Watson, *Romanzoffia* Cham., and *Tricardia* Torr. ex S. Watson (Table 1), which left *P. dalesiana* in an uncertain and isolated relationship with these genera and *Phacelia* (Walden 2010).

The species is easily recognized morphologically as a member of subfamily Hydrophyloideae, but is distinct from other members of tribe Phacelieae and warrants recognition as a separate genus from *Phacelia*. The taxon can be distinguished from *Phacelia* by the combination of perennial, acaulescent habit, axillary few-flowered scorpioid inflorescence, presence of multicellular glandular trichomes with unicellular ellipsoidal heads, deeply parted style, paired pendant ovules, semiorbicular corolla scales, $n = 8$, and tricolpo-

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FIG. 1. Herbert Clair Cantelow, John Thomas Howell and Ella Dales Miles Cantelow on porch at Scott Ranch (1936 photo by grandson Herbert Park Cantelow, courtesy of the Cantelow family and of Ella Dales and Herbert Cantelow papers, California Academy of Sciences Archives).



FIG. 2. Habit of *Howellanthus dalesianus*. Bar = 1 cm.



FIG. 3. Close up of corolla, showing semiorbicular scales at base of filaments. Bar = 1 cm.

rate pollen with exine striato-rugulate (Constance and Chuang 1982; Di Fulvio and Dottori 1995; Di Fulvio et al. 1999; Walden 2010).

TAXONOMIC TREATMENT

Howellanthus (Constance) Walden and R. Patt., gen. et stat. nov. *Phacelia* subg. *Howellanthus* Constance; Madroño 11:198–203. 1953.—Type species **Howellanthus dalesianus** (J. T. Howell) Walden and R. Patt., comb. nov., *hoc loco designatus*. *Phacelia dalesiana* J. T. Howell, Leaflets of Western Botany, 2:51. 1937.—Type: USA, California, Trinity Co., Summit of Scott Mountain, 25 June 1937, A. Eastwood and J. T. Howell 5014 (holotype: CAS!; isotypes CAS!, UCI!, POM!).

Genus habitu *Hesperochiron*, differt cymis laxis paucifloris, vix scorpioideis; trichomata glandulifera, stipula multicellularia, capitata ellipsoidea et unicellularia; corolla alba maculis purpureis in fauce; squamae interstaminales semiorbicularia; filamenta glabra basibus non dilatatis; stylus partitus ad basem; capsula suborbicularis, ovarium quasi divisum placentis parietalibus spissescens, ovulis 2–4, geminatis, pendulis; pollinis grana 3-colporata, striata-rugulata; semina pler-



FIG. 4. Side view of open corolla and unexpanded bud with presence of abundant glandular trichomes. Bar = 1 cm.

umque 2, raro 4, alveolata; chromosomatum numerus $n = 8$; species endemica terrae oriundae ex rupibus ultramaficis.

Perennial herb, 5–15 cm, densely hairy due to presence of two types of trichomes, unicellular eglandular verrucose-walled conical trichomes, and multicellular glandular trichomes with unicellular ellipsoidal heads. Basal leaves rosulate from caudex, caudine leaves alternate, sometimes appearing opposite on stems, reduced upward. Leaf blades oblong to elliptic, simple, margins entire, with lateral incised venation, 10–50 mm long, blades more or less equal to petiole. Inflorescence a lax scorpioid cyme from axils, one- to few-flowered, pedicel 10–20 mm in fruit. Sepals fused at base, lobes 5, unequal, oblanceolate, accrescent, 3–5 mm long in flower, 4–7 mm long in fruit. Corolla 5–10 mm in diameter, campanulate, fused at base, deciduous, white, sometimes fading lavender in age, throat purple-marked. Corolla scales semiorbicular, fused to base of corolla throat but not to filaments, 2 mm long. Filaments adnate to corolla at base, glabrous, slender, included to slightly exserted, 6–8 mm long, anthers purple, pollen tricolporate, colpi nearly smooth, exine striato-rugulate. Style

TABLE 1. TAXONOMIC CHARACTERS OF *HOWELLANTHUS* AND RELATED GENERA.

Character	<i>Howellanthus</i>	<i>Phacelia</i>	<i>Draperia</i>	<i>Hesperochiron</i>	<i>Romanzoffia</i>	<i>Tricardia</i>
Inflorescence	axillary from basal lvs., barely scorpioid	scorpioid	scorpioid	axillary from basal lvs.	scorpioid	scorpioid
Flowers	one–several	several–many annual, biennial or perennial	several–many perennial	solitary perennial	one–many annual or perennial	few perennial
Habit	perennial	generally cauline, alternate	cauline, opposite	basal rosette	generally basal, cauline alternate	generally basal, cauline alternate
Leaves	basal, cauline reduced, alternate	present or absent slender	absent slender	absent broad at base bifid	absent slender	present slender
Corolla scales	present slender	bifid to deeply parted	bifid	barely two-lobed	bifid	bifid
Filaments	slender	1–many	1–4	many	4–8	many
Style	deeply parted	$n = 5, 7–14, 22–24, 33$	$n = 9$	$n = 8$	$n = 11$	$n = 8$
Seed number	2–4	tricolporate	tricolporate	tricolporate	tricolporate	tricolporate
Chromosome number	$n = 8$	unicellular ellipsoidal head	unicellular ellipsoidal head	unicellular ellipsoidal head	unicellular	unicellular
Pollen	tricolporate	multicellular globose head, multicellular globose or oboconic-peltate head	multicellular globose head, multicellular globose or oboconic-peltate head	cylindrical head	cylindrical head	hemispherical head
Capitate glandular trichomes	unicellular ellipsoidal head					cylindrical head

parted nearly to base, included to slightly exserted, 6–7 mm long, glabrous or sometimes pubescent–hairy at base. Ovaries one-celled, ovules paired (2–4 per ovary), pendant. Capsule 4 mm long, subspheric. Seeds 2–4, ovoid, brown, 2.5–4 mm long, surface alveolate, pubescent. $n = 8$. Blooming May–August.

DISTRIBUTION

Howellanthus dalesianus occurs in the Scott Mountains and Trinity Alps, near the junction of Shasta, Trinity, and Siskiyou counties (Fig. 5). The type location is Scott Mountain Summit in Trinity County, intersected by State Highway 3 and the Pacific Crest Trail (Ferlatte 1978). The type locality is the most collected single population represented in herbaria, due to the accessibility provided by the maintained highway and forest trails. However, while the type locality may appear accessible today, we speculate that the species was not collected prior to 1936 due to morphological similarity to *Hesperochiron californicus* (Benth.) S. Watson, which also occurs on Scott Mountain, and the limited presence of botanical collectors in the Scott Mountains prior to 1930.

For three decades Scott Mountain was the only known locality for the species, but currently seven populations have been vouchered in herbaria, although three are from single collections. The USDA National Forest Service Shasta–Trinity and Klamath have surveyed and continue to manage fifty populations for the species on public lands, with additional unvouchered reports of populations on private land holdings in the California Department of Fish and Game Natural Diversity Database (Adamson and Kierstead-Nelson 1991). The USDA Forest Service lists *Phacelia dalesiana* as a sensitive species, and the California Native Plant Society lists *Phacelia dalesiana* as 4.3 (limited distribution, not very threatened in California), California Endemic, S3.3 (vulnerable) and G3 (vulnerable, no current threats known) (CNPS 2010; Showalter 1991).

The elevation of the species ranges from 1600–2200 m, on generally flat topography in openings or dry meadows in upper montane coniferous forest (Adamson and Kierstead-Nelson 1991). All populations are on soils derived from ultrabasic rock associated with the Trinity Ultramafic sheet (Kruckeberg 1984; Adamson and Kierstead-Nelson 1991). *Howellanthus dalesianus* has been documented on disturbed areas, with variation in litter cover within mature populations, although the species requires bare soil for germination and establishment (Adamson and Kierstead-Nelson 1991; Kierstead-Nelson and Engstrom 1991–1993). The species blooms from May to August, with flowering closely tied to snowmelt for a short season, and fruits until late September.

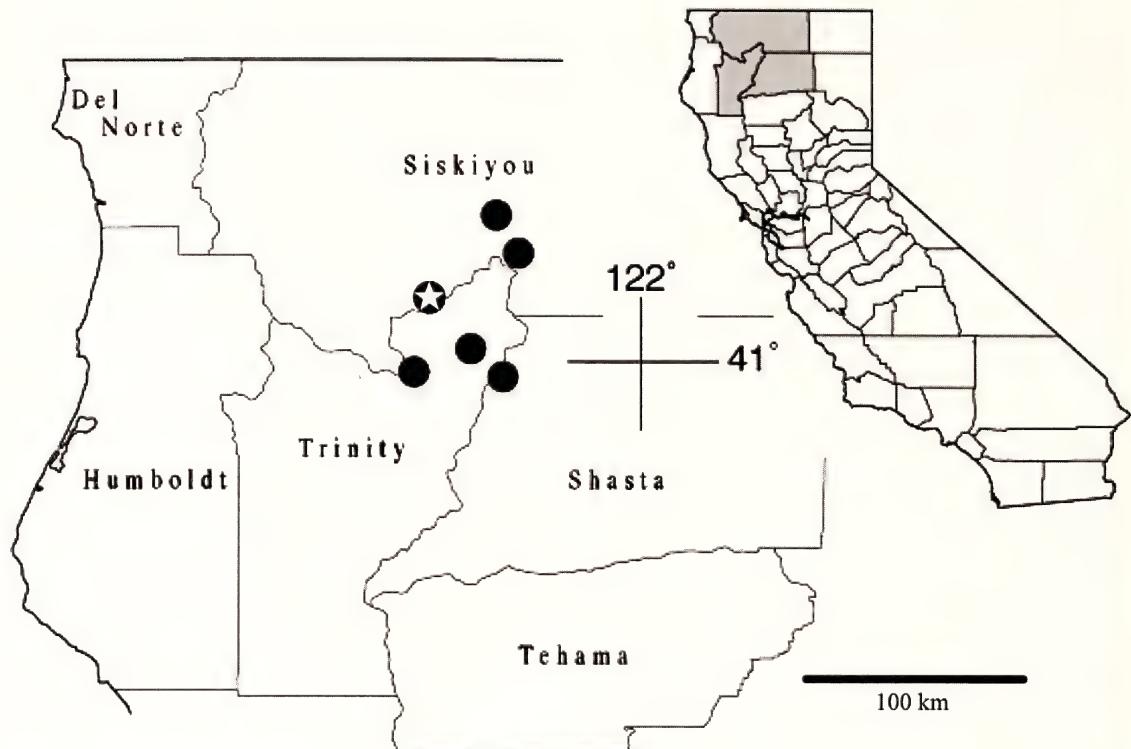


FIG. 5. Distribution of vouchered collections of *Howellanthus dalesianus* in Siskiyou, Trinity, and Shasta counties, California. Starred locality indicates type locality on map.

ADDITIONAL SPECIMENS EXAMINED

USA. CALIFORNIA. Shasta Co.: Trinity Mountains, saddle between Rattlesnake Hill and Chicken Hawk Hill, at summit on Forest Rd 38N21, at Sardine Spring, 15 June 1993, D. W. Taylor (JEPS). Siskiyou Co.: 4 m NE Scott Mountain, trail from Robbers Meadows to Kangaroo Lake, 1 June 1977, S. Horner 110 (JEPS); Mt. Shasta Ranger District, Mumbo Basin at 40N26 and 38N24, 20 June 1991, J. Kierstead 91-68 (ST); Scott Mountain divide, 17 May 1947, H. L. Mason 14773 (UC); Kangaroo Lake Campground, along streams, 25 July 1969, F. W. Oettinger s.n. (CAS, RSA, UC); Kangaroo Lake, 25 July 1967, D. Parker and W. Roderick s.n. (CAS); Scott Mountain Summit, 21 June 2005, R. W. Patterson & S. Santos 1982 (SFSU); Scott Mountain rd summit, upper end of N meadow, 14 June 1963, W. Roderick s.n. (JEPS); Scott Mountain campground, 18 June 2010, G. K. Walden 324 (SFSU); Scott Mountain campground, 7 July 2010, G. K. Walden 332 (SFSU). Trinity Co.: Summit of Scott Mountain, 21 May 1936, E. D. Cantelow 1276 (CAS); Summit of Scott Mountain, 9 June 1939, E. D. Cantelow 2891 (CAS); Summit of Scott Mountain, 23 June 1948, E. D. Cantelow s.n. (CAS); Near Scott Mountain Summit, close to the town of Callahan,

China Mountain quadrangle 1 July 1978, Clifton and Ground 1662 (UC); Summit of rd over Scott Mountain, sandy flat of rocky meadow, 1 June 1946, L. Constance and R. H. Shan 3070 (CAS, UC); Trail from Deer Flat to Shiny Lake ca. 1/4 m above Deer Creek Flat, 8 July 1976, J. DiTomaso 600 (UC); Along USFS trail 8W13 from Deer Flat to Shimmy Lake, 1/4 to 1/2 m E of Deer Flat Camp, 7 July 1976, W. J. Ferlatte and J. DiTomaso 1776 (CAS, JEPS); Summit of Scott Mountain, N of Carrville, 24 August 1936, J. T. Howell 12736 (CAS); Summit of Scott Mountain, N of Carrville, 30 July 1937, J. T. Howell 13691 (CAS); Scott Mountain summit on rd from Carrville to Callahan, 20 May 1980, J. T. Howell, T. C. Fuller and G. D. Barbe 53545 (CAS); Summit of Scott Mountain, rocky serpentine soil, 9 June 1958, D. Parker 649 (CAS, RSA); Scorpion Lake, Trinity Mountains, west-erly upper flank Bonanza King, 13 June 2002, D. W. Taylor 18156 (JEPS). Shasta Co.: Trinity Mountains, saddle between Rattlesnake Hill and Chicken Hawk Hill, at summit on Forest Rd 38N21, at Sardine Spring, 15 June 1993, D. W. Taylor 13656 (JEPS).

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NOTEWORTHY COLLECTIONS

CALIFORNIA

ACACIA DEALBATA Link. (FABACEAE).—Shasta Co., City of Redding, on a large mid-channel gravel bar in the Sacramento River approximately 0.40 km S of the Bonneyview Bridge, associated species include *Populus fremontii*, *Quercus lobata*, *Robinia pseudoacacia*, *Salix lucida* subsp. *lasiandra*, *Salix exigua*, *Rubus discolor*, *Nerium oleander*, *Cytisus scoparius*, *Equisetum arvense*, *Carex barbarae*, and *Cynodon dactylon*, Enterprise USGS 7.5' quadrangle, T31N R4W SE $\frac{1}{4}$ Sec. 18, UTM 10T 0554595E 4487377N, elev. 134 m, 1 December 2010, L. Lindstrand III, s.n. (North State Resources Herbarium¹ [private], CDA); Shasta Co., on upland bluff 0.48 km below Shasta Dam on E side of Sacramento River, associated species include *Ailanthus altissima*, *Quercus kelloggii*, *Pinus sabiniana*, *Robinia pseudoacacia*, *Arctostaphylos viscida*, *Cercis occidentalis*, *Eriodictyon californicum*, *Heteromeles arbutifolia*, and *Cytisus scoparius*, also observed in nearby riparian habitat adjacent to Sacramento River associated with *Salix lucida* subsp. *lasiandra*, *Salix exigua*, *Nerium oleander*, *Cephalanthus occidentalis*, *Fraxinus latifolia*, *Alnus rhombifolia*, *Vitis californica*, and *Rubus discolor*, Shasta Dam USGS 7.5' quadrangle, T33N R5W NE $\frac{1}{4}$ of SW $\frac{1}{4}$ Sec. 15, UTM 10T 0548826E 4507166N, elev. 232 m, 7 December 2010, L. Lindstrand III, s.n. (North State Resources Herbarium¹ [private], CDA); Shasta Co., City of Redding, on a mid-channel gravel bar in the Sacramento River approximately 0.32 km S of the Highway 44 Bridge, associated species include *Quercus lobata*, *Robinia pseudoacacia*, *Salix lucida* subsp. *lasiandra*, *Salix exigua*, *Rubus discolor*, *Equisetum arvense*, *Carex barbarae*, and *Juncus* sp., Enterprise USGS 7.5' quadrangle, T32N R4W NE $\frac{1}{4}$ of SW $\frac{1}{4}$ Sec. 31, UTM 10T 0553553E 4492622N, elevation 140 m, 7 December 2010, L. Lindstrand III, s.n. (North State Resources Herbarium¹ [private], CDA); Shasta Co., City of Redding, along rocky western shoreline of the Sacramento River approximately 0.80 km S of Keswick Dam, associated species include *Ailanthus altissima*, *Quercus wislizenii*, *Robinia pseudoacacia*, *Salix lucida* subsp. *lasiandra*, *Salix exigua*, *Nerium oleander*, *Cytisus scoparius*, *Arctostaphylos viscida*, *Cercis occidentalis*, *Eriodictyon californicum*, *Ceanothus cuneatus*, and *Brickellia* sp., Redding USGS 7.5' quadrangle, T31N R5W NW $\frac{1}{4}$ of NW $\frac{1}{4}$ Sec. 28, UTM 10T 0546918E 4495017N, elevation 152 m, 7 December 2010, L. Lindstrand III, s.n. (North State Resources Herbarium¹ [private], CDA).

Previous knowledge. *Acacia dealbata* is native to southeastern Australia and an invasive species to California. In California the species is known to occur in the western North Coast Ranges, San Francisco Bay Region, western South Coast Ranges, and the South Coast (Hickman 1993; DiTomaso and Healy 2007). The species has also been recorded in the northern Sierra Nevada Foothills in Butte Co. (Calflora 2010). These findings represent the first records of *Acacia dealbata* in Shasta Co., and the northernmost-recorded extent of

the species in interior northern California. At the Shasta Dam site the species was first observed on 4 November 2010, when plant material was collected in the field and given a tentative identification of an unknown *Acacia*. Following further detailed examination, the plant was identified as *Acacia dealbata*. Additional plant material was collected from the site on 7 December 2010. Plant material was collected from the City of Redding sites on 1 and 7 December 2010 when the locations were first observed. Vouchers from all locations were sent to the California Department of Food and Agriculture Plant Pests Diagnostics Center for annotation, where Botany Laboratory staff confirmed the species identification.

Significance. *Acacia dealbata* is included in the 2007 California Invasive Plant Council Invasive Plant Inventory and assigned a “Moderate” rating (Cal-IPC 2006). These findings represent the first recorded observations of *Acacia dealbata* in Shasta Co., and significant (between approximately 160 to 180 km) northern extensions of the known species range in interior California. Multiple age classes, fruiting individuals, and seedlings, were observed at all locations, suggesting these populations reproduce and are capable of expansion.

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OREGON

MATTHIOLA INCANA (L.) W. T. Aiton (BRASSICACEAE).—Clatsop Co., N end of Arch Cape on sandstone cliff overlooking the Pacific Ocean, 45.8233°N, 123.96233°W, elev. 5 m, with *Holcus lanatus*, *Gaultheria shallon*, *Rubus*, *Fragaria*, *Lonicera*, *Festuca*, *Aira*, 16 September 2008, R. R. Halse 7553 (OSC, MO).

Previous knowledge. This European native is a commonly cultivated ornamental. It has become naturalized in California and Texas on ocean cliffs and bluffs and sandy areas (Al-Shehbaz 2010).

Significance. First report for Oregon.

BRASSICA OLERACEA L. (BRASSICACEAE).—Lane Co., along U.S. Hwy. 101 ca. 8.4 m S of Yachats, 44.20830°N, 124.11411°W, elev. 15 m, coastal bluff with *Marah*, *Rubus*, *Equisetum*, *Vicia*, *Gaultheria*, *Heracleum*, 25 May 2010, R. R. Halse 7880 (OSC, duplicates to be distributed).

Previous knowledge. This native of Europe is a commonly cultivated vegetable crop. It has become naturalized in coastal California and in the northeastern U.S. and adjacent Canada (Warwick 2010).

Significance. First report for Oregon.

SCHOENOPLECTUS CALIFORNICUS (C. A. Mey.) Soják (CYPERACEAE).—Lane Co., Siuslaw National Forest, Baker Beach area ca. 7 m N of Florence, 44.09333°N, 124.11920°W, elev. 5 m, very common in

¹ North State Resources, Inc. Herbarium, 5000 Bechelli Lane, Suite 203, Redding, CA 96002.

shallow waters around the edge of Lily Lake with *Ulex*, *Rubus*, *Lysichiton*, *Callitrichie*, *Oenanthe*, *Spiraea*, stems triangular, to 3 meters tall, 9 July 2009 R. R. Halse 7719 (OSC, RSA, WTU, NY).

Previous knowledge. This native species is found in marshes from California eastward across the southern U.S. to North Carolina (Smith 2002).

Significance. First report for Oregon.

ORNITHOPUS PERPUSILLUS L. (FABACEAE).—Lane Co., Washburne State Park, N of Heceta Head, bluff above the beach, on the trail by the picnic area, in *Pinus contorta* woods, common, T16S, R12W, Sec. 22, 7 June 2004, K. L. Chambers 6398, determined by R. R. Halse in 2009 (OSC); same area, Carl G. Washburne Memorial State Park off of U.S. Hwy. 101 ca. 12 m N of Florence, 44.16110°N, 124.11708°W, elev. 14 m, weed around edges of trails with *Picea*, *Vaccinium*, *Maianthemum*, *Gaultheria*, 9 July 2009, R. R. Halse 7723 (OSC, WTU, NY, RSA, VDB); same location, common weed around parking areas with *Trifolium* spp., *Lolium*, *Medicago*, *Vicia*, 25 May 2010, R. R. Halse 7876 (OSC, MU, duplicates to be distributed).

Previous knowledge. This native of Europe is known from Pennsylvania (Rhoades and Klein 1993).

Significance. First report for Oregon.

TRIFOLIUM RETUSUM L. (FABACEAE).—Jackson Co., along State Hwy. 62 near its junction with Corey Road, southern edge of White City, 42.41491°N, 122.85540°W, elev. 398 m, weedy roadside with *Matricaria*, *Erodium*, *Trifolium* spp., *Hordeum*, *Vicia*, *Poa*, 31 May 2010, R. R. Halse 7906 (OSC, MU, duplicates to be distributed).

Previous knowledge. This European native is known from California (Hrusa et al. 2002).

Significance. First report for Oregon.

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PRESIDENT'S REPORT FOR VOLUME 57

Dear CBS member,

The past year has been an exciting time for the Council of the California Botanical Society. The Council this year has moved closer to bringing the Society totally online through the website. The website has been redesigned to update approaches and bring more information to the membership. Please check it out and give us ideas for making it better for you. We have made great progress with *Madroño* thanks to the editors; submission of manuscripts and reviews have now been converted to an online process. Meanwhile, we have a proposal to get all the back issues of *Madroño* available through JSTOR. This year, thanks to the Treasurer, we also established a Finance Subcommittee, staffed by our Treasurer, the Past-President and President. This permits us to establish financial investment goals that might grow our current funds and help us keep future cost increases minimal to the membership.

Given that the California Botanical Society was established in 1913, this upcoming year will represent the 98th year of the Society. Yes, that means we are already planning for the Centennial Celebration of our Society. We have negotiated with the California Native Plant Society to join them in their large meeting in January 2012 and provide the Banquet Speaker for the event. We are looking at 2012 as the initiation of a year of field trips sponsored to

some extent by the Society, perhaps some trips reenacting historic "phyto-jogs" in California's past.

Our membership base is the foundation of the Society and your support allows us to promote botanical research and education. This year, in addition to encouraging other botanists you know to join the Society, we are also hoping to hear from you about your ideas for the celebration of our 100th year. Let us know by emailing or writing to any member of the Council. We're certain that you harbor some incredible ideas for the Centennial!

Increasing our membership is always a priority, so please continue to encourage your colleagues to join us and to publish in *Madroño*. This is especially true of our younger colleagues; as we move online we hope to be more attractive to the younger cohorts of botanists raised in an all-online computer age. Also, please consider providing a sponsoring membership or subscription to a foreign scientist or scientific institution to support botanical research in economically depressed, developing countries. For more information on making such a gift, please contact Corresponding Secretary Heather Driscoll (hdriscoll@berkeley.edu). The Society also welcomes gifts or other contributions to our endowment.

V. Thomas Parker
December 2010

EDITORS' REPORT FOR VOLUME 57

We are pleased to report the publication of this volume of *Madroño* by the California Botanical Society (CBS) in 2010. The journal is continuing to reduce turnaround time, as we now average six months between submission and publication. With the new electronic submission and manuscript review process, we feel we are well on our way to a much smoother review process. As always, we are extremely grateful to all the individuals who serve as reviewers and contribute to the quality of the journal.

This year we received 26 new manuscripts and 24 were accepted for publication. Several manuscripts were also carried over from the previous year. The current volume includes articles (including Notes), new taxa, Noteworthy Collections, and Book Reviews. There was a mix of

systematic and ecological manuscripts submitted. Many of the systematic manuscripts incorporated current molecular techniques and data as well as cutting edge data analysis methods. It is notable that manuscripts reporting taxa new to science are being submitted on a regular basis.

As Editors, we have enjoyed our interactions with contributors and reviewers this past year and look forward to another year of continuing the long and distinguished tradition in botanical publication represented by *Madroño*.

Tim Lowrey
Richard Whitkus
December 2010

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DEDICATION

MICHAEL G. BARBOUR

The California Botanical Society dedicates this volume of Madroño to one of California's most influential plant ecologists, Michael G. Barbour, in recognition of his distinguish accomplishments in research, in teaching, and in conservation. Michael was born in February, 1942. After graduating *magna cum laude* with a BS in Botany in 1963 from Michigan State University, Barbour went on to obtain his doctorate in Botany from Duke University in 1967. Prior to obtaining his doctorate, he was also a Fulbright Fellow in Adelaide, Australia. Michael joined the faculty of the University of California, Davis (UCD) in 1967 and became one of the youngest tenured faculty at UCD. During his 40 years at UCD, he was a professor in a succession of departments (Botany, Plant Biology, Ornamental Horticulture, and finally Plant Sciences, from which position he retired in 2008).

Although California has been his home throughout his career, and has provided the mainstay of his academic pursuits, Michael has conducted or supervised research in many parts of the world, including Argentina, Spain, Portugal, Israel, Mexico, and Australia. A common thread in his career has been exploring the stressors, disturbances, and tolerances that define the habitat limits of different species and vegetation communities.

His work on desert scrub in the southwestern deserts of North America investigated the role of competition for resources in the spatial patterning of species as well as the biogeographic and genetic relationships between *Larrea* in North and South America. His work on salt tolerance of Californian coastal dune and salt marsh plants underscored the interaction of physiology and tolerance in the zonal distribution of species and communities. His work in the red and white fir forests of the Sierra Nevada of California investigated the means by which dominant species in cold and snowy environments displace each other in the major Sierran ecotone at 2000 m elevation.

Working in the Canary Islands, he studied the age structure, stand dynamics, and fire regime of old-growth *Pinus canariensis* forests—a species with a unique set of attributes for a serotinous conifer. Most recently, he completed a study of mixed evergreen forests in central Spain and northern California, teasing out the environmental factors that seemed to explain varying dominance by conifers vs. hardwoods and by particular species, such as *Quercus pyrenaica* and *Q. garryana*.

Research results have been published in the American Journal of Botany, American Midland Naturalist, the Journal of Biogeography, Forest Ecology and Management, Madroño, the Journal of Vegetation Science, Conservation Biology, Israel Journal of Botany, Oecologia, and as chapters in several technical monographs. Michael has published more than 150 books, chapters, and papers.

Michael has taken his academic role seriously beyond his own research. As an educator he has authored or co-authored a diversity of text books on botany, plant ecology, landscape ecology, and vegetation. He took on

the Vegetation of North America with his major professor at Duke, W.D. Billings, and has also co-authored the most widely used texts on plant ecology. He and his long-time UCD friend and mentor, Jack Major, edited and wrote portions of the first two editions of the widely used compendium on vegetation ecology for California (the Terrestrial Vegetation of California), which set the stage for many developments in the study of California and western North American vegetation.

Michael is also a truly gifted teacher. His courses on California plant communities and plant ecology are legendary, involving an expertly crafted marriage of field trips and lectures. His lectures are pitch-perfect matches with his audience, whether laypeople hearing about vernal pools for the first time, or graduate students, learning about the fine points of fire ecology or physiological ecology. Watching him teach, providing clear summary points and artistic real-time chalk board illustrations (he is not too fond of PowerPoint), has been for me a humbling lesson in the art of classical instruction. His capabilities did not go unrecognized by UCD. In 1988, the campus awarded him a Citation for Distinguished Teaching. Michael served as the major professor for 50 graduate students and was a committee member for many others. A number of his ex-students now have important faculty, NGO, federal and state agency positions, or are successful consultants.

Though eternally congenial, even-handed, and humorous, Michael has not shied away from academic debate or conflict. When challenged by European colleagues to get American colleagues to use European methods of vegetation analysis and classification after supporting the development of a new classification system for California's vegetation he invited them over to work with him. As a result, he involved many phytosociologists in the last two decades in the rapid collaborative accumulation of knowledge on our state's vegetation classification and has continued to be a voice for philosophical exchange in



Photo by Brett Hall, September 2009.

the International Association for Vegetation Science. His spirit of information-sharing and openness prevailed in many forms throughout Michael's career. It was important, for example, in his role as the first chair of the Ecological Society of America's Vegetation Panel, where the task was to develop and standardize a single classification system that would be scientifically grounded and adopted by all federal natural resource agencies.

Michael, though academically trained and accomplished, also became involved in a number of conservation issues and has shown many of us the power of promoting conservation through scientifically defensible means. My first encounter with this was as a member of the California Native Plant Society's Plant Communities Committee where he deftly and calmly (though he refutes this) led a disparate group of opinionated ecologists to a shared vision of conservation-based, quantitative vegetation classification. He similarly became involved in an effort to develop a quantifiable approach to vernal pool classification monitoring and evaluation, and from that to putting metrics on vernal pool restoration by quantifying the deviance between created vernal pool communities and naturally occurring ones. After a

decade of work with a team of vernal pool experts, his approach has now been adopted by the U.S. Environmental Protection Agency and other regulatory agencies.

Dr. Barbour is a lucid writer and a perceptive editor, having served on the editorial board of several peer-reviewed journals. He is also not above writing and collaborating on projects that are more literary than they are scholarly. He has co-authored and co-performed with poet Gary Snyder and has co-written several popular articles with his wife Valerie Whitworth on California conservation and natural history. In short, Michael is worthy of all the academic praise he has received, but equally as worthy in his role as a bridger of schisms, a practical, yet passionate spokesperson for the marvelous beauty of nature, and as an all-around citizen of the world.

Michael, it is a pleasure to be given the honor to write this dedication to you.

Todd Keeler-Wolf, Ph.D.
Senior Ecologist
Vegetation Classification and Mapping Program
California Department of Fish and Game

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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2010

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